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Contributors are requested to send Botanical Manuscripts to

Mr W. B. Brierley,

Rothamsted Experimental Station,

Harpenden;

and Zoological Manuscripts to

Mr D. Ward Cutler,

of the same address.

OBSERVATIONS ON THE INSECT FAUNA OF
PERMANENT PASTURE IN CHESHIRE

By HUBERT M. MORRIS, M.Sc.

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Experimental Station, Harpenden.)*

(With 1 Text-fig.)

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1. INTRODUCTION.

THIS investigation was carried out between September 1916 and September 1917, with the object of obtaining as much information as possible with regard to the insect fauna of a permanent pasture. The field in which the investigation was carried out was chosen as being as nearly as possible typical of all such fields in the surrounding district, which comprises the central and eastern parts of Cheshire.

I am indebted to Dr A. D. Imms for assistance in many ways throughout this investigation; to Mr T. J. Young, M.Sc., formerly Principal of the College of Agriculture, Holmes Chapel, Cheshire, for permission to use the field in which it was carried out; and to the following gentlemen for assistance in the identification of many of the insects taken: Mr J. M. Brown, B.Sc.; Mr H. Bury, B.A.; Mr J. Collin; Mr G. T. Lyle; the Rev. F. D. Morice, M.A.; Mr C. Morley; the Rev. J. Waterston, B.D., B.Sc.

The investigation was carried out from the Department of Agricultural Entomology, Manchester University, and the work finally completed at Rothamsted.

2. DESCRIPTION OF THE DISTRICT.

This region is mainly devoted to the production of milk, and a large proportion of the area is occupied by permanent pastures for the grazing of the dairy cattle. The fields in this district are usually small compared with those in other parts of England, about ten acres being a common area.

They are almost universally separated by hedges of hawthorn, often very much overgrown, and overrun with bramble and dog-rose, together with holly and occasionally furze-bushes. These hedges often stand on a low bank and, in addition to the above mentioned shrubs, usually contain a few trees, the commonest being the oak. Similar trees are also often found away from the hedges, scattered about the fields. These hedges and trees give the district, when seen from a distance or from a slight elevation, a very well-wooded appearance, which, however, is not so noticeable on a closer examination. These trees are almost always rather small and stunted owing, probably, to their being scattered about singly and not usually gathered together in woods or coppices.

Another very noticeable feature of the district is the number of ponds which are present, several often being found in a single field. Many of these ponds have formed where pits were dug in order to obtain the marl which underlies this district, and which was formerly spread over the fields, owing to the general shortage of lime in the soil of the district.

The small wood indicated on the map consists of beech, oak, alder, ash, and sycamore, with some holly, hawthorn, mountain ash, and elm, with an undergrowth of elder and hazel.

The crops grown on the arable fields in the immediate neighbourhood during the period of the investigation were:

Field	1916	1917
A	Potatoes; oats	Oats; wheat
B	Wheat; oats	Oats; clover and grass mixture
C	Potatoes; mangolds; swedes	Wheat; oats
D	Wheat; oats; rye grass	Oats; clover and grass mixture
E	Clover and grass mixture	Clover and grass mixture
G	Clover and grass mixture; oats	Mangolds; swedes; oats; potatoes
H	Oats	Clover and grass mixture
I	Clover and grass mixture	Oats
M	Temporary pasture laid down 1914	
N	Nursery of seedling conifers sown 1916, previously pasture	
P	Potatoes	Oats
Q	Oats	Oats
R	Wheat; oats	Swedes; mangolds; clover and grass mixture



Fig. 1. Map of the locality in which the field under observation was situated. Reduced from Ordnance Survey map to a scale of 10.75 inches = 1 mile.

The area marked F on the map is the College garden, in which many kinds of fruit and vegetables are grown. The enclosures marked L are permanent pastures. The enclosure marked O is the field in which the investigation was carried out.

3. DESCRIPTION OF THE FIELD.

The field in which this investigation was carried out forms part of the farm of the Holmes Chapel College of Agriculture, and is known as the "Lane Field." It lies at an altitude of about 220 feet above sea level, and has an area of about 10.2 acres.

The Lane Field is roughly rectangular in shape, the longer sides running almost due north and south, with the shorter sides approximately at right angles to them. The field is surrounded on all four sides by hawthorn hedges, those on the north, east and west sides being well grown, thick, and kept fairly clean. The hedge on the south side is older and thinner, the bushes not having been cut back, and it is more overrun with brambles than the other hedges, and also contains a few furze bushes. In these hedges grow several trees, chiefly oaks, with one or two ashes, sycamores, and alders, and there are also six oak trees in a line east and west across the centre of the field, which, with a slight depression beside which they stand, appear to mark the position of a former hedge, which has been removed many years.

On the west side, near the south-west angle, is a row of three small ponds lying along the boundary of the field, and on the east side a row of five similar ponds lies just on and beyond the boundary of the field, while just outside the south-east corner is a small area which is usually rather swampy, where a similar pond has been filled in.

The field is almost level, there being a slight slope from the east side down to the west, but this does not amount to more than about five feet. The lowest part is the north-western portion which is liable to become water-logged in very wet weather, and may then have water standing in small pools on it for a short time.

The soil of the College Farm "consists almost entirely of a strong loam of Glacial Drift overlying the Triassic rocks. It shows variations in places from a pure Boulder Clay to a lighter class of sandy loam, the latter occurring in small patches here and there, and being more marked round the College buildings and near the main road. There is an outcrop of the underlying Keuper marl along the broken hillside bordering the River Dane, and an area of alluvial deposit immediately adjacent to the stream" (College Prospectus).

The character of the soil of the field varies somewhat, that of the north-western portion probably containing a larger proportion of clay, while that of the south-eastern portion is more sandy.

The Lane Field has been a pasture for at least thirty or forty years, and possibly longer, no one in the neighbourhood appearing to remember it having been ploughed. For several years prior to 1914 the field had received a yearly dressing of bone-meal, but from that date to the period during which the observations were carried out it had been unmanured. The field is regularly grazed by sheep, cattle and horses.

4. CHEMICAL FEATURES OF THE AREA.

It was considered advisable, in order to define the conditions in the selected field as exactly as possible, to carry out both chemical and mechanical analyses of the soil of the field.

Chemical Analysis (in percentages).

Iron (Fe_2O_3)	2.152	Phosphorus (P_2O_5)	0.348
Calcium (CaO)	0.57	Aluminium (Al_2O_3)	2.360
Magnesium (MgO)	0.609	Potassium (K_2O)	0.60
Nitrogen (N)	0.210	Sulphates (SO_3)	0.066

Mechanical Analysis.

Moisture	1.86	Fine sand (0.2 to 0.04 mm.)	28.53
Organic matter	6.21	Silt (0.04 to 0.01 mm.) ...	16.94
Stones (over 3 mm.) ...	0.70	Fine silt (0.01 to 0.002 mm.)	6.71
Fine gravel (3.0 to 1.0 mm.)	1.29	Clay (below 0.002 mm.) ...	4.46
Coarse sand (1.0 to 0.2 mm.)	32.40		

For the above analyses samples of soil were taken from various parts of the field, to a depth of nine inches, these samples being afterwards mixed. At a depth of about a foot a stiff stratum was encountered, which appeared to have a much higher proportion of clay. Below a depth of about six inches there was very little organic matter, which is accounted for largely by the fact that most of the grasses were of the shallow rooted kinds.

5. BOTANICAL FEATURES OF THE AREA.

Relatively few species of plants occurred in the field. The predominant grasses were the Crested Dogs-tail (*Cynosurus cristatus*) and the Bent grasses (*Agrostis* spp.). There were, however, patches where Cocksfoot (*Dactylis glomerata*) and Sweet Vernal grass (*Anthoxanthum odoratum*)

predominated. An analysis of a typical area gave the following results in percentages by weight:

Gramineae

<i>Agrostis alba</i> and <i>A. vulgaris</i>	44.1
<i>Cynosurus cristatus</i>	30.3
<i>Lolium perenne</i>	9.4
<i>Poa</i> spp.	3.5—87.3

Leguminosae

<i>Trifolium</i> spp.	5.6
------------------------------	-----

Other orders (regarded as weeds) 7.0

Under the latter category the following may be mentioned:

Abundant: *Ranunculus acris*, *R. repens*, *Bellis perennis*, *Brachythecum rutabulum*.

Common: *Holcus lanatus*, *Plantago lanceolata*, *Urtica dioica*, *Carduus arvensis*, *Cerastium triviale*.

Occasional: *Polygonum persecaria*, *Plantago major*, *Ajuga reptans*, *Hieracium* spp., *Luzula campestris*, *Rumex acetosa*.

Urtica dioica occurred in two or three patches in the field and also in the hedges in a few places. *Luzula campestris* occurred in the lower and damper part of the field.

The hedge-bottoms were fairly clean owing to those of the College farm being occasionally dug over. In addition to most of the above species, the hedges also contained species of *Rumex*. A moss, probably *Brachythecum rutabulum*, formed an almost continuous covering to the soil, although obscured by the taller plants from casual observation.

6. METHODS OF INVESTIGATION.

The investigation was carried out in the following manner. The turf and soil of an area ten inches square was removed entire to a depth of two inches. The soil below was then removed in layers, each layer being examined separately so that the depth at which the insects occurred could be determined. This examination was carried out in the field, and on several occasions the soil was examined to a depth of two feet, but as very few insects were found at a greater depth than two inches, one foot was usually considered a sufficient depth to examine.

The upper layer, consisting of the turf and surface soil, was placed in a box and taken to the laboratory, as, owing to the presence of roots and of almost all the soil insects, this sample required more careful examination.

Of the larvae and pupae obtained, some were killed and preserved immediately, while an attempt was made to rear the adult insects from the others, on account of the difficulty of identifying larvae. In some cases this was successfully accomplished, but in a number of cases it did not succeed.

In addition to the examination of the insects actually present in the soil, large numbers of adult insects were obtained by sweeping the herbage with a net, a large proportion of which were insects with soil inhabiting larvae, but in addition to these, other species were taken whose presence was due to accident or to their having migrated from their breeding place.

7. INSECTS OCCURRING IN THE SOIL OF THE AREA.

(The figures in brackets indicate the months during which the species occurred; where there are two numbers, the upper indicates the month and the lower the number of individuals found.)

Collembola.

Entomobryidae. *Isotoma viridis* Bourl. Schott (1, 2, 7, 8, 12); *I. olivacea* Tullb. var. *grisescens* (Schaff.) (1, 12); *Isotomurus palustris* (Mull.) (1, 2, 7, 8, 11, 12); *Entomobrya multifasciata* (2, 7); *Lepidocyrtus cyaneus* (12).

Achorutidae. *Onychiurus armatus* (Tullb.) (1); *Achorutes armatus* (Nic.) Tullb. (11); *A. manubrialis* Tullb. (1, 11).

Sminthuridae. *Sminthurus viridis* (Linn.) Lubb. (1, 6, 7, 8, 10); *Sminthurinus aureus* (Lubb.) var. *ochropus* (Reut.) (11); *S. aureus* var. *4-lineatus* (7).

Rhynchota.

Aphidae spp. ($\frac{1}{1}$, $\frac{1}{2}$, $\frac{1}{1^2}$); spp. ($\frac{1}{1}$, $\frac{2}{3}$).

Thysanoptera.

Spp. ($\frac{7}{6}$, 8, $\frac{1}{2}$, $\frac{1}{2^2}$).

Lepidoptera.

Larvae and pupae.

Triphaena pronuba L. ($\frac{1}{1}$, $\frac{1}{1}$); spp. ($\frac{2}{3}$, $\frac{1}{1}$, $\frac{1}{3^2}$).

Coleoptera.

Adults.

Carabidae. *Amara apricaria* Pk. ($\frac{2}{3}$); *Bembidium obtusum* Sturm. ($\frac{1}{1}$); *Olivina fossor* L. ($\frac{8}{1}$, $\frac{1}{1}$); *Anchomenus sexpunctatus* L. ($\frac{1}{1^2}$); *Calathus melanocephalus* L. ($\frac{4}{1}$, $\frac{1}{1^2}$).

Hydrophilidae. *Megasternum boletophagus* Marsh ($\frac{2}{3}$, $\frac{4}{1}$, $\frac{1}{2^2}$).

Scarabaeidae. *Aphodius ater* De G. ($\frac{2}{1}$, $\frac{1}{1}$); *A. contaminatus* Herbst. ($\frac{2}{1}$, $\frac{2}{1}$); *A. fimetarius* L. ($\frac{1}{2}$, $\frac{1}{1^2}$).

Staphylinidae. *Atheta (Homalota) analis* Grav. ($\frac{1}{3}$, $\frac{2}{3}$, $\frac{4}{3}$, $\frac{5}{3}$, $\frac{6}{3}$, $\frac{10}{3}$, $\frac{11}{3}$, $\frac{11}{3}$); *A. (H.) fungi* Grav. ($\frac{1}{3}$, $\frac{2}{3}$, $\frac{3}{4}$, $\frac{5}{3}$, $\frac{7}{3}$, $\frac{12}{3}$); *Tachyporus chrysomelinus* L. ($\frac{1}{3}$, $\frac{2}{3}$, $\frac{11}{3}$, $\frac{12}{3}$); *T. hypnorum* Fab. ($\frac{1}{3}$, $\frac{11}{3}$); *T. humerosus* Erich. ($\frac{10}{3}$, $\frac{11}{3}$, $\frac{12}{3}$); *Tachinus laticollis* Grav. ($\frac{11}{3}$); *T. rufipes* De G. ($\frac{1}{3}$, $\frac{11}{3}$); *Philonthus laminatus* Creutz ($\frac{1}{3}$); *P. varius* Gyll. ($\frac{1}{3}$, $\frac{12}{3}$); *Gabrieus* sp. ($\frac{12}{3}$); *Othius melanocephalus* Grav. ($\frac{11}{3}$, $\frac{12}{3}$); *Xantholinus linearis* Oliv. ($\frac{1}{2}$, $\frac{8}{3}$, $\frac{9}{3}$, $\frac{12}{3}$); *Stenus brunnipes* Steph. ($\frac{11}{4}$, $\frac{12}{2}$); *Platystethus arenarius* Fourc. ($\frac{11}{3}$, $\frac{12}{3}$); *Oxytelus sculpturatus* Grav. ($\frac{1}{3}$).

Elateridae. *Agriotes obscurus* L. ($\frac{1}{2}$, $\frac{2}{3}$, $\frac{12}{3}$).

Chrysomelidae. *Longitarsus luridus* Scop. ($\frac{3}{3}$, $\frac{11}{3}$); black var. ($\frac{2}{3}$).

Byrrhidae. *Simplocaria semistriata* Fab. ($\frac{8}{3}$, $\frac{9}{3}$).

Curculionidae. *Apion virens* Herbst. ($\frac{1}{3}$, $\frac{2}{3}$); *Sitones puncticollis* Steph. ($\frac{7}{3}$, $\frac{11}{3}$).

Larvae and pupae.

Carabidae. Sp. ($\frac{10}{3}$).

Scarabaeidae. Sp. ($\frac{8}{2}$, $\frac{11}{3}$).

Staphylinidae. *Tachyporus* ($\frac{7}{3}$, $\frac{10}{3}$); *Quedidus* ($\frac{2}{3}$, $\frac{7}{3}$); *Xantholinus* ($\frac{3}{3}$, $\frac{7}{11}$, $\frac{8}{3}$, $\frac{10}{3}$, $\frac{11}{2}$); other species ($\frac{7}{3}$).

Elateridae. *Agriotes* ($\frac{1}{2}$, $\frac{2}{4}$, $\frac{3}{4}$, $\frac{8}{3}$, $\frac{9}{3}$).

Curculionidae. *Sitones puncticollis* Steph. ($\frac{6}{10}$, $\frac{7}{4}$); other species ($\frac{1}{3}$, $\frac{8}{3}$, $\frac{7}{2}$, $\frac{9}{2}$, $\frac{10}{3}$, $\frac{11}{2}$, $\frac{12}{2}$).

Diptera.

Larvae and pupae.

Mycetophilidae. Sp. ($\frac{1}{12}$, $\frac{2}{9}$, $\frac{3}{6}$, $\frac{4}{8}$, $\frac{10}{8}$, $\frac{11}{8}$).

Bibionidae. *Bibio Johannis* L. ($\frac{1}{4}$, $\frac{2}{4}$, $\frac{3}{10}$); *Bibio* sp. ($\frac{9}{48}$).

Tipulidae. *Tipula* sp. ($\frac{1}{3}$, $\frac{11}{3}$, $\frac{12}{3}$).

Stratiomyidae. *Odontomyia felina* Pz. ($\frac{3}{3}$).

Leptidae. *Leptis* sp. ($\frac{10}{11}$).

Anthomyidae. *Phorbia ignota* Rond. ($\frac{8}{3}$); sp. ($\frac{7}{2}$, $\frac{8}{3}$, $\frac{11}{3}$).

Hymenoptera.

Larvae and pupae.

Tenthredinidae. *Dolerus fissus* Htg. ($\frac{2}{3}$).

Ichneumonidae. *Amblyteles armatorius* Forst. ($\frac{1}{3}$).

Larvae belonging to the following families were found at a greater depth than two inches: *Coleoptera*. Scarabaeidae, 2 to 6 ins. ($\frac{1}{2}$); Curculionidae, 2 to 4 ins. ($\frac{10}{3}$); 2 to 4 ins. ($\frac{41}{3}$), 2 to 6 ins. ($\frac{11}{3}$); family not det. 2 to 6 ins. ($\frac{1}{3}$). *Diptera*. Mycetophilidae, 2 to 6 ins. ($\frac{11}{8}$); family not det. 4 to 8 ins. ($\frac{10}{2}$).

8. ADULT INSECTS ASSOCIATED WITH THE HERBAGE OF THE AREA AND TAKEN BY SWEEPING.

Collembola.

Sminthuridae. *Sminthurus viridis* (Linn.) Lub. (6, 8, 10).

*Rhynchocha.**Homoptera*—Cercopidae. *Philaenus spumarius* L. (6).Acocephalidae. *Acocephalus nervosus* Schr. (9).Jassidae. *Cicadula sexnotata* Fall. (6, 7, 9).*Heteroptera*—Capsidae. *Megaloceraea ruficornis* Fourc. (7); *Lygus pratensis* Fab. (7); *Psallus lepidus* Fieb. (6).*Lepidoptera.*Pieridae. *Pieris napi* L. (7); *P. rapae* L. (7); *P. brassicae* L. (7).Nymphalidae. *Vanessa urticae* L. (8).

Pyralidae. Spp. (7).

*Coleoptera.*Carabidae. *Pterosticus vulgaris* L. (7); *Bembidium obtusum* Sturm. (9); *Notiophilus aquaticus* L. (7).Hydrophilidae. *Cercyon flavipes* Fab. (6); *Megasternum boletophagus* Marsh (9); *Cryptopleurum atomarium* Oliv. (10).Scarabaeidae. *Aphodius fimetarius* L. (9, 10); *A. fossor* L. (6).Staphylinidae. *Atheta (Homalota) analis* Grav. (9); *Tachyporus hypnorum* Fab. (9); *T. humerosus* Erich. (9); *Mycetophagus splendens* Marsh (4); *Quedidus attenuatus* Gyll. (9); *Philonthus varius* Gyll. (4); *P. sordidus* Grav. (6); *Oxytelus sculpturatus* Grav. (10); *O. lacqueatus* Marsh (6).Nitidulidae. *Meligethes aeneus* Fab. (6); *Brachypterus urticae* Fab. (6, 8).Telephoridae. *Telephorus nigricans* Müll. (4); *T. bicolor* Fab. (6); *T. flavilabris* Fall. (6).Chrysomelidae. *Longitarsus luridus* Scop. (8, 9, 10); *Plectrocelis concinna* Marsh (7); *Phyllotreta undulata* Kuts. (9).Curculionidae. *Apion virens* Herbst. (9, 10); *Phyllobius pyri* L. (4); *P. alneti* F. = *urticae* De G. (4); *Sitones puncticollis* Steph. (9, 10); *Caeliodes quadrimaculatus* L. (6).*Diptera.*

Mycetophilidae. Sp. (3, 6).

Bibionidae. *Dilophus febrilis* L. (9); *D. albipennis* Mg. (6); *Bibio Marci* L. (6).Simuliidae. *Simulium latipes* Mg. (10); *S. maculatum* Mg. (6); *Simulium* sp. (7).Tipulidae. *Tipula oleracea* L. (6, 9); *T. paludosa* Mg. (8); *Pachyrrhina histio* F. (6).Stratiomyidae. *Beris vallata* Forster (6, 7); *Chloromyia formosa* Scop. (6); *Sargus flavipes* Mg. (8).Tabanidae. *Haematopota pluvialis* L. (6); *Chrysops caecutiens* L. (6).Leptidae. *Leptis scolopacea* L. (6); *L. tringaria* L. (7); *Chrysopilus auratus* F. (6).Empidae. *Empis trigramma* Mg. (6, 7); *Hilara* sp. (7).Dolichopidae. *Dolichopus unguulatus* L. (6); *D. longitarsus* Stan. (6).Lonchopteridae. *Lonchoptera lutea* Pz. (9, 10, 12).Syrphidae. *Liogaster metallina* F. (8); *Platycheirus scutatus* Mg. (6); *Platycheirus* sp. (8); *Syrphus albostrigatus* Flin. (8); *S. ribesii* L. (8); *S. balteatus* De G. (8); *Melanostoma mellinum* L. (6, 8); *Syrphid pipiens* L. (6); *Eristalis horticola* De G. (6); *E. arbustorum* L. (8).

- Sepsidae. *Sepsis cynipsea* L. (6, 7).
 Opomyzidae. *Opomyza germinationis* L. (6, 9).
 Oscinidae. *Chlorops* spp. (7).
 Borboridae. *Borborus geniculatus* Mg. (1, 6); *Borborus* sp. (1).
 Cordyluridae. *Scatophaga stercoraria* L. (6, 8, 10).
 Anthomyiidae. *Spilogaster duplariis* Stien. (9); *S. quadrimaculata* Fln. (10);
Hyetodesia sp. (6); *Phorbia ignota* Rond. (6, 7); *Hydrophoria ambigua* Fln. (6, 8);
Homolomyia serena Fln. (7); *Hydrotaea palaestrica* Mg. (6); *Hylemyia strigosa* F. (7);
Hylemyia sp. (6, 7).
 Muscidae. *Morellia hortorum* Fln. (6); *Stomoxys calcitrans* L. (9); *Onesia cognata*
 Mg. (6); *Mesembrina meridiana* L. (6, 8); *Lucilia caesar* L. (8).
 Sarcophagidae. *Sarcophaga carnaria* L. (8); *Graphomyia maculata* Scop. (8).
 Tachinidae. Sp. (8).

Hymenoptera.

- Tenthredinidae. *Dolerus niger* Klug. (6); *Taxonus glabratus* Thoms. (6); *Selandria serva* Ste. (6, 7).
 Cynipidae. *Figites nitens* Hartig (7, 9).
 Ichneumonidae. *Atractodes gilvipes* Hilgr. (7); *A. vestalis* Hal. (7); *Mesoleius aulicus* Grav. (7); *Platylabus dimidiatus* Grav. (6); *Phygadeuon fumator* Grav. (7);
P. variabilis Grav. (7); *Hemiteles tristator* Grav. (7).
 Braconidae. *Aspilota nervosa* Hal. (7); *Dacnusa misella* Marsh (7); *D. areolaris*
 Nees. (9); spp. (7, 9).
 Vespidae. *Vespa germanica* Fab. (7, 8).
 Apidae. *Andrena cineraria* L. (6); *Nomada alternata* Kirby (6); *Nomada* sp. (6);
Bombus terrestris L. (7).
 Chalcidae. *Tetrastichus* sp. (9); *Gonatocerus* sp. (7); *Eucyrtus* sp. (7); *Eulophus*
 sp. (6).
 Proctotrypidae. *Diapria* sp. (9); *Lagynodes*, probably *L. pallidus* Boh. (8).

9. NOTEWORTHY SPECIES IN THE INSECT FAUNA.

Rhynchota.

The most abundant species belonging to this order was *Cicadula sexnotata* Fall. which occurred in very great numbers during the months June to September. *Philaenus spumarius* L. was also abundant. The other species of Rhynchota were only occasionally taken. *Psallus lepidus* Fieb. had probably wandered from one of the ash trees on the border of the field.

Neuroptera.

The only representative of this family was *Sialis lutaria*, which occurred near the ponds.

Lepidoptera.

Few species of Lepidoptera were met with in the field, adults and larvae of Pyralidae being the most numerous. Larvae of *Triphaena pronuba* L. occurred in the soil and a pupa of this species was parasitized by the Ichneumon *Amblyteles armatorius* Forst.

Coleoptera.

The family Staphylinidae was quite the best represented, both in point of species and of actual numbers, the commonest species being *Atheta (Homalota) analis* Grav. A few species such as *Brachypterus urticae* Fab., *Phyllobius urticae* De G. and *Caeliodes quadrimaculatus* L. occurred especially on or near the patches of *Urtica dioica*.

"Wireworms," the larvae of *Agriotes obscurus* L. occurred very frequently, especially in the rougher parts of the field.

The presence of the Scarabaeidae, both adults and larvae, and of the Hydrophilidae was probably due to the patches of dung about the field owing to its having been grazed by cattle and horses.

Apion virens Herbst. and *Sitones puncticollis* Steph. occurred abundantly in the parts of the field in which clover was present. Larvae and pupae of the latter species were taken at the roots of clover, the larvae of the former probably occurring in the same situation.

The single specimen of *Phyllotreta undulata* Kuts., which was obtained, had probably wandered from one of the fields of swedes in the neighbourhood, the nearest being at the east end of field C (Fig. 1).

Diptera.

Larvae belonging to the family Mycetophilidae were frequently met with in the soil, where they sometimes occurred in masses. In one sample of soil 107 Mycetophilid larvae were met with, in another 58 were found.

Larvae of the family Bibionidae also occurred in large numbers, but not so frequently as was the case with the Mycetophilidae; on one occasion 49 larvae of *Bibio Johannis* L. were found in a single sample of soil, and on another occasion 464 larvae of a species of *Bibio*.

Tipula oleracea L. and *T. paludosa* Mg. were fairly numerous but their larvae were not met with very frequently.

Anthomyiidae were numerous, especially in the adult state.

Hymenoptera.

Of the Tenthredinidae which occurred, the most plentiful belonged to the genus *Dolerus*. *Selandria serva* Ste. also occurred several times.

A fair number of parasitic Hymenoptera were taken, usually in the adult state, a specimen of *Amblyteles armatorius* Forst. was, however, reared from a pupa of *Triphaena pronuba* L.

The following are the hosts which have been recorded for the different species of parasitic Hymenoptera (*vide* Morley 1903-1914):

Atractodes gilvipes Hlgr.; recorded from larvae of *Acidalia marginepunctata* Göze.

Atractodes vestalis Hal.; host not recorded.

Mesoleius aulicus Grav. Bred in Europe from *Nematus fulvus*, *Selandria ovata*, *Cladius viminalis*, *Lophyrus pini* L.

Platylabus dimidiatus Grav. Bred from *Depressaria heracleana* and *D. depressella* on the Continent. In this country it has been bred from *Melanippe fluctuata* and *M. montanata*.

Phygadeuon fumator Grav. Bred from *Mamestra brassicae*, probably preys mainly on Anthomyiidae.

Phygadeuon variabilis Grav. Reared from Dipterous (probably Tachinid) pupae.

Hemiteles tristator Grav. Has been bred from *Pieris brassicae* and *Limneria* cocoons among the eggs of *Epeira diademata*, *Fumea intermediella* and *Solenobia triquetrella*.

The Braconid *Aspilota nervosa* Hal. is stated to be parasitic on *Homalomyia* (*Fannia*) *canicularis*.

A nest of *Vespa germanica* Fab. occurred on the bank of one of the ponds on the west of the field, and individuals from this and other nests in the neighbourhood were frequently met with in the field.

A number of burrows of *Andrena cineraria* L. occurred in a colony on a small smooth area of bare soil between two of the ponds. These burrows were found in the autumn to contain larvae, adults of both sexes, and other larvae which probably belonged to a parasitic species of *Nomada*, these bees having been seen in the neighbourhood of the burrows during the summer.

10. DISTRIBUTION IN DEPTH.

Relatively few insects, and those all in the larval state, were found at a greater depth than two inches, and none deeper than six inches.

This may be partly due to the fact that the soil was very compact owing to the field having been a permanent pasture for many years. The grass roots, although they formed a solid turf at the surface, did not descend to any depth, as the predominant grasses of the field were shallow-rooted species, and although there was a certain amount of organic matter below the two inch level, there was very little below the six inch level. Even when the ground was covered with three or four inches of snow the insects did not appear to have descended to any greater depth than usual, and when, during a period of hard frost the ground was frozen to a depth of about four inches, it did not appear to cause any change in the depth to which the insects penetrated.

The latter depth in any given area is probably controlled by four factors: depth to which their particular food occurs, aëration, moisture and temperature of the soil. In the present instance the food of both carnivorous and vegetarian forms depended ultimately on the presence of organic matter, either living plants or their decaying remains, this material, as has been noted above, only being present, except in a very small proportion, in the upper six inches, and particularly in the upper two inches.

Owing to the soil not having been disturbed for a considerable time, it had become very much compressed, and consequently the aëration of the soil would be poor, and again, owing to the very stiff subsoil, the rain was not able to drain away readily, in some parts of the field even forming pools on the surface.

As has been mentioned above, the difference in temperature between the upper and lower levels of the soil appeared to have little effect on the insects.

Thus the first three conditions were distinctly unfavourable to deep penetration of the soil by the insects in this case, while the fourth condition was found to have little effect on the depth to which insects descended.

Of the four factors given above, the first, the occurrence of the particular food required by the insect, is largely controlled by the flora of the area, while the second and third, aëration and moisture respectively, are largely controlled by the texture and composition of the soil, which in turn influences the flora. Other factors the influence of which on the insect fauna must be considered are light, wind, rainfall, atmospheric pressure, altitude, exposure and slope. In the present instance these factors do not require to be considered in detail as they would be practically uniform over the district of which the area under observation was selected as being typical.

11. DISCUSSION OF PREVIOUS WORK.

It is noticeable that in this investigation many fewer species were met with than were recorded by Cameron (1917) in his investigation in the same district. This difference is largely accounted for by the fact that in the present instance care was taken to select an environment as uniform as possible, in which little invasion by insects not belonging to the area under observation would occur. In the former case the area was of a very composite nature and included a small wood and fields under various crops. In addition, his two pastures were much "rougher" than that now dealt with, containing a much larger proportion of weeds, and patches of long grass. In his earlier work (1913), Cameron also dealt with an area which was not uniform, and included a field which had been artificially levelled and a small orchard, with several decaying logs and vegetable refuse.

In both the above cases there was a much greater variety of food available, and consequently many more species of insects were present, and there was also considerable variation in the texture of the soil in different parts of the area.

It is rather remarkable that a greater number of individuals should have been found in this field than in either of the fields in the same district examined by Cameron, which are marked Lc and N on the map.

This is possibly due, in the case of "Glover's Meadow," to the absence of dung from the field, as that substance attracts many species, including the species of *Bibio*, to which the high figure obtained in the present area was partly due. With the "Alluvial Pasture," the difference may be due to its tendency to be marshy throughout the year, which condition is unfavourable to soil insects.

12. CENSUS OF SOIL INSECTS.

During the investigation twenty-nine samples, each with a superficial area of 100 square inches, were examined, and a total of 1658 insects were obtained. From this figure the total number of insects in an acre of the field works out at 3,586,088, which is probably somewhat below the actual number, as with small insects like *Collembola* and *Thysanoptera*, it is difficult to be sure of securing every specimen, and a proportion of the more active forms of the other families probably effect their escape during the removal of the soil.

The numbers of the different orders were: *Collembola*, 566,680; *Rhynchota*, 15,140; *Thysanoptera*, 43,258; *Lepidoptera*, 15,140; *Coleoptera*, 744,038; *Diptera*, 2,193,180; *Hymenoptera*, 8652.

The figure for *Diptera* is considerably increased by the finding on one occasion of 464 larvae in a sample, but about 50 larvae were not infrequently met with in a sample of soil.

Among notably injurious species the numbers per acre work out as follows: *Agriotes*, larvae 114,634, adults 8652; larvae and pupae of *Triphaena pronuba* L. 4326; larvae of *Tipula oleracea* and *T. paludosa* 19,466.

The numbers of insects per acre found by Cameron, as calculated from the figures he gives, are 835,560 for "Glover's Meadow," and 1,537,046 for the "Alluvial Pasture." M'Attee, working near Washington, U.S.A., calculated that on an acre of forest floor there were 1,216,880 animals belonging to *Insecta*, *Arachnida* and other *Arthropoda*, *Annelida* and *Gastropoda*; similarly in an acre of meadow land in the same locality he calculated that there were 13,654,710 animals.

As this figure includes *Arachnida* and other *Arthropoda*, *Annelida* and *Gastropoda*, it cannot be compared with the figure obtained in the present instance.

13. SUMMARY.

1. An area was chosen which was as typical as possible of the permanent pasture fields of the district, and in which invasion by insects not belonging to the area would be reduced to a minimum.

2. In order to define the characters of the area under consideration as clearly as possible, chemical, mechanical and botanical analyses were carried out.

3. Insects, largely in immature forms, were obtained by examining samples of soil from various parts of the area, and in addition many adults were obtained by sweeping the herbage with a net. The latter method produced also some invading forms which did not belong to the area.

4. The factors influencing the distribution by depth of the insects in the soil were in this case chiefly occurrence of food, aëration, and moisture, and the result of these influences was that the insects seldom penetrated even as deep as six inches, the vast majority of specimens being found at a depth not greater than two inches.

5. The census of insects actually found in the samples of soil gave an insect population of 3,586,088 per acre. The family best represented in number of individuals was the Bibionidae, species of which made up 32.4 per cent. of the total number of soil insects. The next in number were the Mycetophilidae 16.7 per cent., and the Staphylinidae 12.2 per cent. With regard to number of species occurring in the soil, the Coleoptera, with 29 species, was the best represented order.

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“DAMPING OFF” AND “FOOT ROT” OF TOMATO SEEDLINGS

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“DAMPING OFF” is a term commonly used by nurserymen to describe the death of very young seedlings. In the seed-boxes, the young seedlings are attacked at the base, and the rapid collapse of the stem tissues at this point causes the seedlings to fall over.

“Foot Rot” is the term applied when the young plants are attacked at a later date. In this case the seedlings grow strongly in the seed-boxes, but are attacked after “potting up” or even after “planting out” in the houses. As in the case of “damping off,” the base of the stem is attacked, and these tissues collapse causing the plant to fall over.

Generally the highest death rate has occurred after periods of watering, and this has led growers to draw a close connection between the disease and damping, and has given rise to the name “damping off.” Properly speaking, the term applies to a fatal disease set up through the agency of parasitic fungi, but it is often made to embrace the wilting of seedlings caused by some injurious chemical or physical factor in the soil. These latter causes of death are of somewhat rare occurrence, and when they do take place may usually be traced to carelessness on the part of the workman.

Cresylic acid, which is extensively used in the winter for sterilising the wood-work, staging and soil itself in the glass houses, has occasionally been known to produce a wilt of young plants, when the proper precautions necessary in such sterilisation have been disregarded. In one instance, an insufficient time had elapsed between sterilising the propagating benches and the raising of seedlings upon them. The result was that the seedlings were stunted in growth and turned a blue-green colour; many were so scorched in the stem that they fell over and had all the appearances of “damped off” seedlings.

In another instance a quantity of undiluted cresylic acid had been upset in one part of a house by a workman, who omitted to report the accident. In due course the house was planted, and, while the greater

number of the individuals grew quite healthily, it was observed that in one spot all the plants died. These showed all the symptoms usually associated with the disease caused by *Phytophthora cryptogea*, but examination showed that no pathogenic organisms were present in the diseased tissues. Further inquiries led to the knowledge that the area containing the dead plants was that in which the cresylic acid had been upset.

The deleterious effect which ammonia has upon plant growth is frequently observed, and in no place, perhaps, is the result so marked as in the glass houses where high temperatures prevail. In the early stages of the tomato crop examples can frequently be seen of "damping off" effects produced through the rapid diffusion of ammonia from soil which contains dung not sufficiently matured.

The investigations to be described have been directed towards the congeries of diseases caused by pathogenic fungi.

SOURCES OF INFECTION.

At the outset one is faced by a number of possible sources of infection all of which require careful investigation if complete control of the disease is to be effected. The seeds themselves, the seed-boxes and soil, the stages upon which the boxes rest, and the water used in cultivation are all possible sources of infection.

The Seeds.

It is well known that the coverings of many seeds carry fungus spores which germinate in the soil and destroy the young root as it emerges. The tomato seed is especially suitable for carrying spores, for its testa, being provided with long hairs, easily holds small particles.

Apart from this, the method usually employed by the practical man for the extraction of seeds from the fruits, increases the suspicion as to the purity of the seed. Certainly the best fruits are chosen for the purpose, but the subsequent treatment renders the seed liable to a great deal of contamination. The fruits are first divided in halves and the seeds with the mucilage which surrounds them are cut out into a pail. In order to facilitate the removal of the mucilage, the whole mass is allowed to ferment and soon becomes a mass of putrefaction, forming a pabulum for all kinds of fungi and bacteria. This part of the process is perhaps the most open to criticism because of the opportunity it offers for the rapid growth of any organism, pathogenic or otherwise, that may be carried to the fermenting matter. The length of time the mucilage

and seeds remain in this state varies considerably, but experiment shows that three or four days are sufficient to destroy the mucilage and allow of its easy removal. It is unnecessary and undesirable to allow too long a time for this preliminary rotting of the mucilage. After the fermentation the seed is washed and dried. To reduce the possibility of infection the extraction should be carried out under hygienic conditions, and away from the vicinity of the growing plant where there is danger of contamination from fungus spores in the air. The fruit should be wiped with a rag containing a little lysol or cresylic acid or sprayed with a 2 per cent. solution of formaldehyde in order to sterilise the outside. It must then be well washed, dried and carried to some clean shed or room, where the air is still, and there the seed should be removed.

An examination of many different samples of seed has shown that they carry on their testas a very varied fungus flora, but so far we have been unable to find any active parasites. This, of course, does not prove that tomato seeds never carry destructive organisms but it indicates that such is a rare occurrence. The hairiness of the seed coat and the presence of many fungus spores point to the fact that disease organisms may be carried also. In this connection it is interesting to note that I. Massee¹ has described the presence of hibernating mycelium of *Macrosporium solani* underneath the seed coat in samples of tomato seeds she examined. It is advisable to test all bought seed in a trial box under sterile conditions some time before the general sowing. Seed suspected of impurity should be sterilised. Home produced seed should be free from disease, provided it is derived from the best fruits and has been extracted under hygienic conditions.

Seed-boxes and Pots.

General observation and experimental work show that the disease organisms are carried over from one season to the next by seed-boxes and pots. Discolouration and destruction of plant roots has frequently been traced to some crack or crevice in the pot or box which has harboured the resting spores of the fungus.

The Soil.

The organisms producing “damping off,” like many others, spend part of their existence in the living plant and the rest in hibernation over the winter in the decomposing soil humus. So far as we have been able to determine, “damping off” of tomato seedlings is produced by

¹ Massee, I. *Kew Bulletin*, No. 4, 1914.

three different organisms which appear to be *Phytophthora terrestris* (Sherbakoff)¹, *Ph. cryptogea* (Pethybridge)² and *Rhizoctonia solani* (Kuhn) Duggar³ respectively, though precise identification is not possible until comparisons of pure cultures are completed. *Ph. terrestris* also produces "buck-eye" rot of tomato fruits, stem rot and "foot rot" of the tomato, and stem rot of the lupin. *Ph. cryptogea* has been described⁴ as producing "foot rot" of the tomato and aster, and not infrequently it is very destructive to antirrhinums and lupins. *Rhizoctonia solani* is regarded as a universal soil organism, which attacks young plants.

The Water Supply

Observations in nurseries where epidemics of "damping off" and "foot rot" have been in progress led us to suspect the water as being an important source of infection. Preliminary experiments on seedlings on which water suspected of contamination had been used confirmed this suspicion. We have therefore undertaken an extensive analysis of nursery waters in the Lea Valley to ascertain what organisms pathogenic to the tomato they contain. The results, which will be given in a further communication, show that while some waters are practically free from pathogenic organisms, others contain the spores of many tomato parasites. The problem of pure water supply is exceedingly important and requires very careful investigation. One important and obvious precaution is to avoid all danger of polluting the well by surface drainage from the nursery, or any allotment, garden, etc.

EXPERIMENTAL.

An examination was made of diseased seedlings from various nurseries in the district. The pathogenic organisms were identified, isolated in pure culture and tested for pathogenicity.

The dominating pathogen, here called *Phytophthora* "A," appeared to be identical with *Phytophthora terrestris* described by Sherbakoff⁵ in America as producing "buck-eye" rot of tomato fruits and stem rot of citrus trees and lupins, and is probably identical with *Ph. parasitica*

¹ Sherbakoff, C. D. *Phytopath.*, vol. VII, No. 2, 1917.

² Pethybridge, G. H. and Lafferty, H. A. *Sci. Proc. Roy. Dubl. Soc.*, vol. XV (N.S.), No. 35, 1919.

³ Duggar, B. *Ann. Mo. Bot. Gard.*, vol. II, 1915.

⁴ Pethybridge, G. H. and Lafferty, H. A., *loc. cit.* Spinks, G. T. *Ann. Rept. Agr. and Hort. Res. Sta., Long Ashton, Bristol*, 1917. Robinson, W. *Ann. App. Biol.* vol. II, 1915.

⁵ Sherbakoff, C. D. *Loc. cit.*

described by Dastur¹ in India as attacking castor bean plants. Nearly equal in importance is *Phytophthora* “B,” probably *Ph. cryptogea*, which has been described by Pethybridge and Lafferty² as producing a “foot rot” of the tomato plant. In a few cases *Rhizoctonia solani* was the causative organism. Samples of soil were then obtained from several nurserymen and tested for their power to produce “damping off.” Throughout the whole of our experiments sterile seed-boxes (14"×9"×2"), soil at the rate of five pounds per box, disease-free seed selected by sifting, and sterile water were used. Seed-boxes were “made up” from the soil samples and seeds were sown in the usual manner. Where “damping off” occurred, one or more of the above mentioned fungi was invariably found.

Table I.

Soil	No. of boxes	Parasitic organism
From trade nurseries	10	Phytophthora “A”
” ”	3	Phytophthora “A” and <i>Rhizoctonia solani</i>
” ”	5	Phytophthora “B” and <i>Rhizoctonia solani</i>
” ”	6	Phytophthora “B”
New turf	3	No disease
Old turf (station)	3	”
” (trade nursery)	3	Phytophthora “A”
Old cucumber borders	3	No disease
” ”	3	Phytophthora “A”
Tomato house (station)	3	”
Tomato house sweepings (station)	3	”
Sandy subsoil	3	No disease
Baked soil	3	”
Steamed soil	3	”

Preparation of infected soil to be tested.

The naturally infected soil used for the whole of the experiments described in this paper was obtained from a nursery where “damping off” had been very destructive. The soil was placed under cover on a flat surface and spread out in a layer of some six inches deep. It was thoroughly broken up and mixed with a spade. Next it was divided into eight small heaps and each heap thoroughly worked in turn. Heap 1 was then added to heap 2 and the combined heap well mixed. Heap 3 was then added to heaps 1 and 2 combined and so on until the whole soil was worked into one heap.

¹ Dastur, J. F. *Memrs. Dept. Agr. India, Bot. Series*, vol. v, No. 4, 1913.

² Pethybridge, G. H. and Lafferty, H. A. *Loc. cit.*

Probable error of the average percentage of diseased seedlings per box.

Twelve boxes were each given 5 lbs. of infected soil per box, soaked with water, sown with 100 seeds selected by sieving, and covered with a layer of soil. The percentage germination of the seeds sown and the percentage diseased of those which germinated was ascertained. The seedlings were removed as soon as they became diseased in order to eliminate the factor of lateral spread, and each experiment was brought to a close at the end of 14 days.

From the percentages set down below the probable error of the mean of twelve results was calculated.

% diseased per box	Difference between each result and the mean	(Difference) ²
42	-2.8	7.84
43	-1.8	3.24
44	-0.8	0.64
44	-0.8	0.64
44	-0.8	0.64
45	+0.2	0.04
45	+0.2	0.04
45	+0.2	0.04
45	+0.2	0.04
46	+1.2	1.44
47	+2.2	4.84
48	+3.2	10.24
Mean = 44.8		Sum = 29.88

$$\text{Probable error of each result} = 0.67 \sqrt{\frac{29.88}{11}} = \pm 1.102.$$

$$\text{Probable error of the mean} = \frac{\pm 1.102}{\sqrt{12}} = \pm 0.29.$$

From the above results it will be seen that the percentage of diseased seedlings per box varied from 42 to 48, while the mean was 44.8. This makes the probable error of each result 1.1 and the probable error of the mean 0.29. This result is typical of the results obtained from the whole of the experiments in this paper. In no case was there a wide divergence from the mean and the mean can therefore be taken as an adequate measure of the effect of the particular "limiting factor" under investigation.

Experiments were set up to test the effect of different methods of making up the seed boxes upon the incidence of the disease. The standard method was to weigh out 5 lbs. of soil into each box. Then the soil was compacted by means of a builder's board, soaked with water, 100 seeds

per box were sown and covered with a thin layer of sterile soil. In certain instances, however, sand, lime or charcoal was used in place of the sterilised soil. In other cases a layer of sand, lime or charcoal was put on over the sterile soil, and in still other cases the soil was mixed with different proportions of sand, lime or charcoal. A parallel set of experiments was set up at the same time, using sterilised soil. Diseased seedlings were removed from the boxes as soon as they were attacked in order to eliminate the factor of superficial spreading of the disease. The results of these experiments are shown in Table II.

In the above experiments the soil sample, its weight, the sterility of the seed-boxes, the seeds, the temperature, the barometric pressure, the quality and quantity of the light, and the quantity of sterile water given to each box were constant factors. The limiting factors were solely those indicated in the above table. An examination of the percentage germination columns shows that the difference between the lowest percentage germination and the highest is fairly constant and the remainder of the results are symmetrically placed about the mean. The percentage diseased seedlings showed a similar arrangement. This further indicates that the average percentage results can be taken as accurate measure of the experiment in question.

A covering of sand, charcoal or lime either alone or above a covering of sterile soil produces only a small increase or decrease in the percentage of diseased seedlings per box. Charcoal has no effect, when put on as a covering to the seeds. Sand reduced the percentage diseased by 20 per cent., while lime increased it by 25 per cent. Five per cent. of charcoal added to the soil has a distinctly beneficial effect, for, besides reducing the percentage of diseased seedlings by 25 per cent., it produced a fine crop of sturdy dark green seedlings. A further increase in the amount of charcoal added is not advisable, for it only increased the difficulty of keeping the soil at an even degree of moisture. Certainly a decrease in the percentage of diseased seedlings is induced but this is obviously caused by the increased proportion of sterile particles in the soil. In the case of lime, whether it is added as a covering to the seeds or mixed with the soil itself it increased the percentage of diseased seedlings by nearly 50 per cent., and appears actually harmful. This is in agreement with the fact that the parasitic organisms grow best in a neutral medium.

The relation of the closeness of sowing to the spread of the disease.

In order to ascertain the correct closeness to sow the seeds, and the effect of closeness of sowing upon the incidence of the disease the

Table II

Treatment	No. of boxes	Infected soil				Sterilised soil			
		Lowest % germ.		Highest % germ.		Lowest % germ.		Highest % germ.	
		Aver. %	Lowest %	Aver. %	Highest %	Aver. %	Lowest %	Highest %	Aver. %
Seed covered with $\frac{1}{4}$ " sand	12	95	92	97	36	33	37	95	92
" " $\frac{1}{4}$ " charcoal	12	97	93	99	47	45	48	96	93
" " $\frac{1}{4}$ " lime	12	96	93	98	66	64	68	95	94
" " $\frac{1}{4}$ " sterilised soil	12	96	94	99	45	42	49	97	95
" " $\frac{1}{4}$ " infected soil	12	97	93	99	47	43	50	—	—
Seed covered with $\frac{1}{4}$ " sterile soil and then $\frac{1}{4}$ " sand	12	95	92	96	39	36	41	96	94
" " $\frac{1}{4}$ " charcoal	12	94	90	96	45	43	48	97	95
" " $\frac{1}{4}$ " lime	12	97	92	100	60	58	61	96	94
" " $\frac{1}{4}$ " lime and charcoal	12	96	93	99	53	51	54	97	96
Seed covered with $\frac{1}{4}$ " sand then $\frac{1}{4}$ " charcoal	12	95	92	97	40	37	42	96	95
95 % soil + 5 % charcoal	12	97	92	100	33	29	35	97	96
75 % " + 25 % "	12	96	92	98	25	22	28	97	95
50 % " + 50 % "	12	94	91	98	20	18	25	95	92
95 % " + 5 % lime	12	98	93	100	69	66	71	97	94
75 % " + 25 % "	12	95	92	99	51	49	54	96	95
90 % " + 5 % lime + 5 % charcoal	12	97	93	99	37	34	39	96	94

following experiments were made. Seeds were sown in infected soils in thickness varying from 600 to 25 seeds per box, in sets of four boxes at each degree of thickness. In half the boxes the seedlings were removed, as they were attacked, to eliminate the factor of spread. The remainder were untouched and gave some indication as to the rate of superficial spread of the fungus. The results obtained are shown in Table III.

Table III.

No. of seeds per box	Average % diseased seedlings removed when attacked	Average % diseased seedlings not removed
600	51	100
300	45	100
200	49	100
100	42	78
50	37	46
25	35	41

The second column of the above table shows the uniform results obtained when the seedlings were removed as they were attacked. It indicates that the number of seedlings primarily attacked depends upon the number of disease centres in the soil and not upon the closeness of sowing, when the factor of superficial spread of the organisms is eliminated. The third column where the fungi were allowed to spread is of great practical interest, and shows that the rate of spread of the organism is more rapid, where the seeds are closely sown, than where they are thinly sown. In the closer sowings the density of the plants increases the film of water adhering to the seedlings and offers a ready means of spreading the disease through the box.

Sowing above fifty to the box should be avoided as this materially assists the disease.

The relation of the time and method of watering to the incidence of the disease.

Boxes were "made up" in the usual way, using 5 lbs. of infected soil from the stock heap, sowing 100 seeds per box and removing the seedlings as they became diseased. As soon as the seedlings appeared, the glass covers were removed and the different methods of watering were commenced. For top watering in the morning, midday and evening, 200 c.c. of sterile water were given to each box on every alternate day. For bottom watering the boxes were placed for five minutes each in a zinc tray filled half an inch deep with water. One set of boxes was placed on damp earth in a tray on the staging and received no direct watering after their first soaking preparatory to sowing. The soil upon which they rested

was kept moist, and the seed-boxes obtained their moisture by capillary attraction. The results of these experiments are shown in Table IV.

Table IV.

Method of watering	No. of boxes	No. of seeds per box	Average % diseased
Top watering—evening	12	100	42
" mid-day	12	"	54
" morning	12	"	45
Stood continuously in tray of water	12	"	73
Bottom watering, when necessary	12	"	27
Placed on damp earth	12	"	12

The foregoing experiments indicate that either morning or evening watering is preferable to midday watering and that bottom watering is preferable to top watering. The high percentage of diseased seedlings obtained where the boxes were stood continuously in water emphasises the intimate relation between the rapid progress of the disease and a high water content of the soil. Excellent results were obtained by placing the boxes upon damp earth and allowing them no water except what they obtained by capillary attraction from the earth below. Under such conditions the percentage of diseased seedlings was reduced from 45 per cent. to 12 per cent.

The effect of potash, phosphates and nitrogen upon the incidence of the disease.

In order to test the effect of different manurial treatments upon the incidence of "damping off," 0.5 per cent. of sulphate of potash, nitrate of soda and superphosphate was added to the soil either singly or in different combinations.

100 seeds per box were sown, covered in the usual way, and the seedlings removed as soon as they became diseased.

Table V.

Treatment	No. of boxes	No. of seeds per box	Average % diseased
11 gms. K_2SO_4 per 5 lbs. soil	10	100	11
" $NaNO_3$ " "	10	100	49
" super. " "	10	100	43
11 gms. K_2SO_4 and 11 gms. $NaNO_3$ per 5 lbs. soil	10	100	45
" " super. " "	10	100	29
" $NaNO_3$ and 11 gms. super. " "	10	100	51
Control	10	100	45

The results tabulated above indicate that superphosphate and nitrate of soda have but little effect upon the disease. On the other hand a dressing of 11 gms. of sulphate of potash per 5 lbs. of soil, brought about a considerable reduction in the average of diseased seedlings; this result serving once more to emphasise the power of suitable dressings of potash to restrict fungus diseases.

Fungicides.

In these tests the boxes were made up in the usual way, using infected soil; 100 seeds per box were sown and covered; the fungicidal solutions in the quantities shown in Table VI were then applied from a copper sprayer. The boxes were left until the seeds germinated, when the percentage germination and the percentage diseased seedlings were determined. Each diseased seedling was removed as it fell over.

Table VI.

Treatment	No. of boxes	Average germination	Average % diseased seedlings
Control	6	97	45
400 c.c. 2% solution of copper sulphate	6	9	25
" 1% " "	6	37	43
" $\frac{1}{2}$ % " "	6	94	41
" 2-3-50 Bordeaux mixture	6	95	37
" 4-4-50 " "	6	93	28
" 4-4-100 " "	6	97	39
" 2-3-50 Burgundy mixture	6	92	39
" 1 in 25 formaldehyde solution	6	0	—
" 1 in 50 " "	6	0	—
" 1 in 100 " "	6	93	40
" 1 in 250 " "	6	95	47
" 0.75% solution of sodium fluoride	6	25	7
" 0.5 % " "	6	98	23
" 0.1 % " "	6	96	43
" 0.5 % solution of barium polysulphide	6	93	47
" 0.01% " phenol	6	95	45
$\frac{1}{4}$ oz. " sodium chloride (sprinkled over the soil)	6	97	39

The results obtained indicate that none of the solutions tested are able to control the disease, without injury to the plants.

Control of the disease by soil sterilisation.

Sterilisation of the soil by heat or formaldehyde has proved the most effective method of controlling "damping off."

Sterilisation by steam.

Twelve boxes of naturally infected soil and twelve of inoculated soil were made, six of each being steamed for two hours and the remaining twelve being left untreated to serve as controls. After cooling the whole twenty-four boxes were sown in the usual manner, 100 seeds per box, and the seedlings removed as soon as they became diseased. The seedlings in the steamed soil were perfectly healthy, while the unsteamed controls showed an average of 47 per cent. of diseased plants in each box. Apart from the control of the disease the steamed soil gave much the best type of seedlings. They were more healthy and vigorous and showed better root development than those in the untreated soils. The steaming also killed all the weeds.

Sterilisation by baking gave similar results.

Sterilisation by formaldehyde.

Formaldehyde has long been recommended as a soil fungicide. The soil in the boxes was saturated with different concentrations of formaldehyde; it was then covered for 48 hours to allow the vapours to act. After this time had elapsed the covers were removed and the soil allowed to dry, and seeds were then sown in the usual way. The results are shown in Table VII.

Table VII.

Strength of sterilising solution				Average number of diseased seedlings per box
1 c.c.	40%	formaldehyde	per 200 c.c. water	44
1	"	"	150 "	45
1	"	"	100 "	42
1	"	"	75 "	37
1	"	"	50 "	0
1	"	"	25 "	0
1	"	"	10 "	0

Our results show that all strengths of formaldehyde solutions from 2 per cent. upwards are effective in soil sterilisation, but the weaker solutions are not sufficiently strong to completely sterilise the soil. Our untreated controls in the above experiments gave an average of 48 per cent. diseased seedlings. Further experiments showed that complete sterilisation of the diseased soil could be carried out by the following method. A formaldehyde solution is made by adding one ounce of commercial formalin (40 per cent. formaldehyde) to $2\frac{1}{2}$ pints of water (*i.e.* 1 in 50). The soil is saturated with this solution, covered with glass

for 48 hours, and allowed to stand uncovered for 10 days to make sure all the formaldehyde has evaporated. The seed is then sown in the usual manner. So long as the water is not infected this treatment will ensure a healthy batch of seedlings.

The Seed-box as a Carrier of Disease.

Twenty-four boxes in which "damping off" had been very severe were used. Twelve were left untreated as controls and the remaining twelve were soaked for ten minutes in a 2 per cent. solution of formalin contained in a tub. They were then placed in a heap and covered with sacking for 48 hours in order to allow the vapours of the formaldehyde to act upon the fungi present in the boxes. After this time the sacking was removed and the boxes allowed to dry. All the boxes both treated and untreated were then made up with sterilised soil, sown with sterilised seed, watered with sterile water and placed on sterilised glass plates in the greenhouse. The plants grown in the sterilised boxes were perfectly healthy and showed no signs of "damping off," while eleven boxes out of twelve untreated showed an average of 14 per cent. diseased seedlings.

The results of this experiment, which are given in Table VIII, show that seed-boxes carry the infection from one season to another.

Table VIII.

Date	Untreated boxes	Treated boxes
7. 8.19	Seed sown	Seed sown
20. 8.19	One box showed disease	All boxes with healthy plants
30. 8.19	Five boxes showed disease	" " "
7. 9.19	Nine boxes showed disease	" " "
23. 9.19	Eleven boxes showed disease	Two diseased seedlings in one box
7.10.19	Eleven boxes showed disease	" " "
	One box with healthy plants	

The Pot as a Carrier of Disease.

Twelve pots which had previously contained plants attacked by "foot-rot" were obtained from a nursery. Six were treated with a 2 per cent. solution of formalin in the same manner as the boxes in the previous experiment, while six were left untreated to serve as controls. In four of the six untreated pots the plants developed "foot-rot," while in all the six treated pots the plants remained perfectly healthy.

Sterilisation by formaldehyde of the soil in heaps.

The soil used in the experiment was naturally infected soil obtained from a nursery; and when tested was found to produce the disease quite

readily. Two heaps were made, each of 60 lbs.; one was left untreated and into the other was gradually worked 2 gallons of a 2 per cent. solution of formalin, the whole being thoroughly mixed with a spade. It was then covered with sacking for 48 hours, after which the sacking was removed and the heap spread out and allowed to dry. Fourteen days after treatment, nine boxes and six pots were filled from each heap. The boxes were sown with sterile seed and the pots planted with young healthy seedlings reared in sterilised soil. In each case sterile water was used for watering. The treated soil produced plants free from disease, while the untreated soils in the nine boxes showed an average of 48 per cent. of diseased plants and five pots out of six contained plants affected with "foot-rot."

The time after treatment at which it is safe to sow.

Twenty-four boxes were made up with naturally infected soil. Twenty were treated with a 2 per cent. solution of formalin, covered, and sown in pairs on successive days. One hundred seeds were sown per box, and the infected seedlings were removed as soon as they were attacked.

Table IX.

Time of sowing	Percentage germination	Percentage diseased
On removing covers	49	0
1 day after	57	0
2 days after	69	0
3 "	51	0
4 "	100	0
5 "	97	0
6 "	98	0
7 "	93	0
10 "	94	0
14 "	98	0

The untreated controls showed an average of 44 per cent. diseased seedlings per box.

In this experiment it was safe to sow from four to seven days after treatment, but in practice it is better to allow a fortnight interval for the vapours to pass completely out of the soil.

Treatment after disease has appeared.

Numerous attempts have been made to stop the disease once it has become established in the seed-box. In our experiments, the diseased

seedlings were removed and the remainder were sprayed with different fungicides or treated as indicated in Table X. The only treatments that resulted in an appreciable reduction of the disease were those of copper sulphate with lime, and formaldehyde with ammonia. Ten parts of dry powdered lime obtained from freshly slaked lime, and one part of copper sulphate were ground to a fine powder and thoroughly mixed. After passing through a fine sieve the mixture was sprinkled thinly over the soil. By this treatment only 7 per cent. of diseased seedlings resulted.

When formaldehyde and ammonia are mixed an impure solution of hexamethylene tetramine is produced. In the tests, commercial formalin (containing 40 per cent. formaldehyde) was added to a strong solution of ammonia, .880, in the correct proportions to produce a 40 per cent. solution of hexamethylene tetramine. This was diluted to various concentrations, and 400 c.c. watered on the boxes. The most suitable strength to use proved to be a 0.5 per cent. solution. By its application the percentage of diseased seedlings was reduced to 11. Experiments with older plants "potted up" in diseased soil showed similar results.

Table X.

Treatment		Average % diseased
Compound used	Quantity per box	
Mixture of equal parts of charcoal and lime sprinkled over the soil	$\frac{3}{4}$ oz. per sq. ft.	44
10 parts lime and 1 part copper sulphate sprinkled over the soil	"	7
Sodium fluoride (0.5% solution)	400 c.c.	43
" (0.75% solution)	"	Injured seedlings
Formaldehyde (1% solution)	"	Killed seedlings
" (0.5% solution)	"	34
" (0.13% solution)	"	43
Sodium nitrate (0.5% solution)	"	45
Sulphate of potash (0.5% solution)	"	32
Sulphuric acid (1% solution)	"	Killed seedlings
" (0.25% solution)	"	"
" (0.125% solution)	"	42
" (0.05% solution)	"	44
Citric acid (0.5% solution)	"	40
" (1% solution)	"	41
" (2% solution)	"	43
Hexamethylene tetramine (5% solution)	"	Killed seedlings
" (1% solution)	"	"
" (0.5% solution)	"	11

CULTURAL METHODS OF CONTROL.

The control measures first described, namely soil sterilisation, are those of prevention and cannot be applied after the seed is sown.

It is clear that a certain amount of infection comes from the use of contaminated water, and in nurseries where this has been proved to be the case, it is highly important to obtain a clean water supply.

If the disease has started when the plants are growing, the application of a mixture of 10 parts of lime and 1 part of copper sulphate, put on the soil at the rate of $\frac{3}{4}$ oz. per square foot, has been found to be useful in keeping down the disease. The use of hexamethylene tetramine shows promising results, and further work on this compound is in progress.

The Moisture Factor.

A relatively high percentage of moisture in the soil and the air favours the rapid spread of the "damping off" organism. Careful regulation of the watering, so as to keep the seed-boxes uniformly moist and good ventilation of the propagating houses to dry out the surface soil, will produce the best moisture conditions for checking the disease.

Temperature.

The optimum temperature for growth of *Ph. terrestria* = *Ph. parasitica* is about 30° C. (86° F.), and that of *Ph. cryptogea* and *Rhizoctonia* about 25° C. (77° F.). Below 12° C. (54° F.) the growth of all three is very slow. When the disease has started among the plants, the grower should therefore endeavour to keep the temperature as low as possible without impairing the health of his crop.

Further work is in progress upon the physiological relations of the disease organisms to their environment, and upon their reaction to certain chemical compounds; also upon the method of cleansing contaminated water.

The author takes pleasure in thanking Mr W. B. Brierley of the Rothamsted Experimental Station for the many helpful suggestions and criticisms he has so kindly given him.

CONCLUSIONS

1. "Damping off" of tomato seedlings is a communicable disease due to a group of pathogenic organisms, particularly species of the genus *Phytophthora*.

2. The organisms do not occur in all soils but exist as a definite infection in some.

3. Infection of the seedlings comes primarily from the soil and from water.

4. Seed-boxes and pots may carry on the infection from one season to the next.

5. High temperature and careless watering are frequently responsible for the rapid spread of the disease. By sowing no thicker than fifty seeds to the box, carefully regulating the watering, picking out diseased seedlings, reducing the temperature as much as possible, and giving sufficient ventilation, the disease may be reduced to a minimum.

6. Soil sterilisation by heat or by formaldehyde completely frees the soil from the disease organisms, and thus, provided the water is non-infective, gives protection. In order to ensure a healthy crop of seedlings, all seeds should therefore be sown and “potted up” in sterilised soil.

7. The application of a fine mixture of 10 parts of dry slaked lime and 1 part of copper sulphate at the rate of $\frac{3}{4}$ oz. to the square foot is useful in reducing the amount of the disease.

ON THE OCCURRENCE IN BRITAIN OF THE CONIDIAL STAGE OF *SCLEROTINIA MESPILI* SCHELL.

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(With Plate XI and 2 Text-figures.)

WHILE engaged in an investigation of the Brown Rot diseases of fruit trees in this country the writer was informed that for a number of years medlar trees (*Mespilus germanica* L.) in a cherry orchard near Sittingbourne, Kent, had suffered from a disease supposed to be a form of Brown Rot. The grower was asked to send specimens to Wye College in the event of the reappearance of the disease and in the middle of April of the present year (1920) medlar shoots were received, the leaves of which showed dark-brown blotches varying in size from about 1 cm. in diameter upwards; in a few cases the whole leaf was affected and completely withered. No organism was visible on the surface of the leaves when received but, on placing the specimens in a moist chamber, grey tufts appeared on the upper surface of one of the dead leaves within four days. Microscopic examination showed the tufts to consist of chains of rather large spherical conidia; many of the conidia floated free when placed in a drop of water but others were seen to be connected by slender fusoid bodies and it was at once realised that the fungus was the conidial stage of one of the Sclerotinias of the *S. Linhartiana* type, *i.e.* those in which the conidia become separated by "disjunctors." This term was introduced by Woronin¹ who found and described the development of these bodies in *Sclerotinia Vaccinii*.

The diseased leaves emitted a strong sweetish odour which was particularly noticeable on opening the glass case in which such leaves had been confined for two or three days. Healthy leaves kept under similar conditions did not give off this characteristic odour.

No record could be found of the occurrence of this disease in Britain²,

¹ Woronin, M. "Die Sklerotienkrankheit der Vaccinienbeere," *Mém. de l'Acad. de St Pétersbourg*, Série 7, T. xxxvi, 1880.

² The author is indebted to Miss E. M. Wakefield and Mr J. Ramsbottom for their aid in consulting literature at the Kew Herbarium and at the Natural History Museum respectively.

but reference to Continental mycological literature showed that a similar disease and fungus had been recorded for Switzerland and described in an interesting paper by Schellenberg¹ in 1907. He had observed the diseased condition of the leaves in the open in 1905 and induced the development of the conidial fructifications on diseased leaves which he had collected; in the following year he found the apothecial form, which he named *Sclerotinia Mespili*, on mummified medlar fruit and described the mode of infection of medlar leaves by the ascospores. Schellenberg remarked on the peculiar odour given off from diseased leaves and stated that it attracts insects which carry the conidia (the "chlamydospores" of Schellenberg) to the medlar flowers and so cause infection of the latter. He attributed the odour to the conidial fructifications ("so zeigen diese Chlamydosporenrasen einen ausgesprochenen, starken Duft²"), but the present writer found that diseased leaves on which conidia had not yet appeared were decidedly odoriferous, and a more probable explanation of the phenomenon is that it is caused by an enzymic secretion of the fungus acting on one or more organic compounds present in the tissues of the leaves.

A few days after the specimens were received a visit was paid to the orchard with the object of ascertaining the source of infection, particularly as Schellenberg's work suggested that the spring infection of the leaves is caused by ascospores discharged from apothecia which develop from mummified fruit lying on the ground. The diseased trees were three in number and on each of them about 25 per cent of the flowering shoots were affected, from one to three leaves on each shoot showing the characteristic blotches (Fig. 1); in some cases two distinct spots were found on the same leaf. No conidial fructifications could be found on the leaves on this occasion so that it would appear that the brown areas represented primary infections, and although there must have been some hundreds of such primary infection spots on each tree, the source of infection was not discovered. Numerous undeveloped mummified fruits had remained on the trees from the previous year, but no conidial fructifications, corresponding to those which later developed on the leaves, could be found on them. Similar mummified fruits were found on the ground, but, although a careful search was made no apothecia were discovered.

Towards the end of the same month (April), medlar shoots with leaves

¹ Schellenberg, H. C. "Ueber *Sclerotinia Mespili* und *Sclerotinia Ariae*," *Cent. für Bakt. Abt. 2*, Bd xvii, 188-202, 1907.

² *L.c.*, p. 193.

similarly affected were sent in from Faversham; on some of these shoots as many as four leaves were infected and, in a few cases, the discoloration had extended from the laminae along the petioles and into the axes of the shoots. During May further specimens showing the same disease were obtained from Maidstone, Margate, and Weston-super-Mare (Somerset)¹. The diseased trees at Faversham and Maidstone (one large tree in each case) were examined by the writer early in May; by this time conidial fructifications were to be seen on some of the diseased

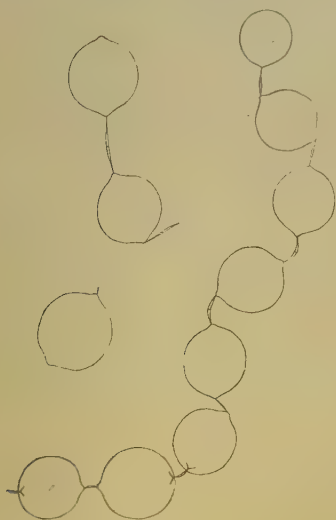


Fig. 1.

Fig. 1. Conidia and disjunctors ($\times 500$).

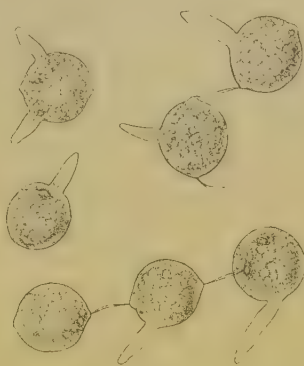


Fig. 2.

Fig. 2. Conidia germinating in distilled water ($\times 500$).

leaves in the open. These fructifications were again confined to the upper surface of the leaves and were sometimes in the form of small, scattered, grey tufts, but usually these soon became confluent to form continuous patches or strips which generally followed the lines of the midrib and chief veins (Plate XI, fig. 2).

The conidia were approximately isodiametric; the longitudinal axis was generally a little longer than the transverse because of the polar papillae, which were from 0.5 to 2μ in length, usually about 1μ . Conidia

¹ Mr W. F. Emptage kindly supplied me with specimens from Weston-super-Mare.

produced on a leaf in the open were measured and found to be from $12 \times 10.5\mu$ to $25 \times 20.5\mu$ (mostly $18-22 \times 16-20\mu$), with an average (of 100 conidia) of $19.3 \times 17.1\mu$; these dimensions are in close conformity with those given by Schellenberg which are $15-18-20\mu$.

The disjunctors were from $3-11\mu$, or more, in length (usually $6-9\mu$); one conidium was attached to its neighbours by disjunctors 14 and 15μ long respectively, and one disjuncor as long as 17μ was observed, but such instances were exceptional. Schellenberg writes, "Der Disjuncor zwischen den einzelnen Sporen wird kräftig ausgebildet und misst $1.5-2\mu$ "; his illustration of a conidial chain however shows disjunctors $3-5.5\mu$ in length.

Some of the mummified fruits (or rather flowers, since they had remained practically undeveloped) were collected from the trees and examined microscopically; mycelium was found within the tissues, and agar cultures obtained from such mycelium resembled those produced from conidia. Particles of the superficial layers of these mummified flowers, when teased out in water, yielded numerous minute (about 3μ in diameter), spherical, spore-like bodies which are probably the "microconidia" described by Schellenberg. Similar microconidia or "sporidia" are produced by the fungus in agar cultures. In size and mode of development they resemble the microconidia produced by *Sclerotinia cinerea* and *S. fructigena* when these are cultivated under laboratory conditions, and also in the fact that they are not known to germinate.

The macroconidia however germinated readily in distilled water and germ tubes about 20μ long were produced within four hours, some of the germinating conidia being still attached to one another by the disjunctors (Text-fig. 2). They also germinated on prune juice agar and on agar prepared with a decoction of medlar leaves, but growth was very slow as compared with that of *Sclerotinia fructigena* or *S. cinerea* when growing on agar culture media. These cultures of *S. Mespili* produced pustules of microconidia but no macroconidia. On agar containing an extract of medlar leaves the cultures were dark brown and the browning extended into the culture medium in advance of the hyphae.

The apparent strict specialisation of the fungus is a feature of practical interest. Two of the outbreaks occurred on medlar trees growing in cherry orchards and the owners were desirous to know whether the medlar leaves were likely to prove a source of infection for the cherries. *Sclerotinia Mespili* is not known to attack cherry trees, but there is no experimental evidence to show that it is unable to do so. In this connection

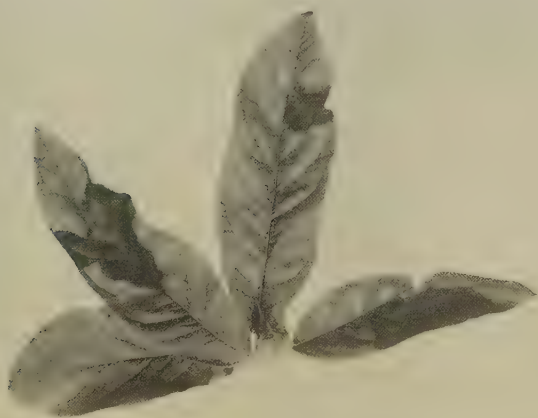


Fig. 1.



Fig. 2.

Schellenberg writes¹, "Auch die Specialisation des Pilzes ist, wie mir scheint, eine weitgehende, denn der Pilz geht nicht auf die nahe verwandte Quitte über und wie es scheint auch nicht auf *Crataegus*, *Pirus malus* und *communis* und *Prunus Padus*, *avium* und *cerasus*."

On the other hand the writer found on one of the medlar trees a mummified flower bearing three pustules of *Monilia cinerea* and also a leaf with numerous pustules of the same fungus; the medlar therefore under certain conditions may serve as a host for *Sclerotinia cinerea* and so become a source of infection for neighbouring plum and cherry trees.

SUMMARY.

This article records the occurrence, in the spring of 1920, of the conidial form of *Sclerotinia Mespili* Schell. on the leaves of medlar trees in four localities in Kent and one in Somersetshire.

Mycelium obtained from dead flowers which had remained on the tree from the previous year gave rise to cultures similar to those obtained from conidia taken from infected leaves but the *Sclerotinia* stage of the fungus was not observed.

DESCRIPTION OF PLATE XI

Fig. 1. A young flowering shoot of medlar showing three infected leaves ($\times \frac{1}{4}$).

Fig. 2. A diseased medlar leaf showing the conidial fructifications extending along the mid-rib and chief veins of the infected portion ($\times \frac{2}{3}$).

¹ *L.c.* p. 195.

FRIT FLY (*OSCINIS FRIT*) IN RELATION TO BLINDNESS IN OATS

By A. ROEBUCK.

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(With Plate XII.)

INTRODUCTION.

THE West Midlands, in common with many other areas in the country, suffers severely from the terrible scourge Frit Fly, and every year apparently one can find fields of oats ruined by its depredations.

During extensive observations on frit flies and oat crops since 1913, I have often noticed a considerable number of "blind" spikelets in the panicles on infested fields.

The continued association of these "blind" spikelets on attacked crops, whereas good crops with little or no trace of the fly show no signs of them, naturally suggests some connection, direct or indirect, with *Oscinis frit* itself.

The suggestion that the spring attack on the tillers so weakened the plant as to render it incapable of nourishing all the flowers produced is scarcely tenable. A comparison of oats with other members of the Gramineae would almost indicate that weakness in the plant would show itself more particularly in the bottom or top spikelets, the middle ones being usually well nourished, but "blindness" is found anywhere on the panicle.

Similarly in cases of severe grain attack to consider "blindness" due to an early larva destroying the flower as soon as produced and finding insufficient nourishment moving off to other flowers, is unconvincing. The "blind" spikelets are already produced when the panicle unfurls and therefore before the eggs can have been laid in the ears. Moreover, careful examination of the behaviour of larvae in the grain attack has not shown one case where the flowering glumes and palea are destroyed.

The larvae migrate in the spikelets as the food is exhausted and attack very young flowers but the glumes and palea are left.

The only insects I have found in or around these "blind" spikelets have always been those which were apparently sheltering, or possibly attracted in the early season by these white patches in an otherwise uniform green background.

Continuing observations on this problem the following facts were obtained during the summer of 1919 which point to a direct connection between the "blindness" and frit fly.

OBSERVATIONS.

The Blindness, Deafness or White Ear referred to is most noticeable comparatively early in the season when the oat panicles are unfurling from the sheath and are a good deep green colour. The "blind" spikelets then stand out clearly almost white. They consist almost always of the two flowerless glumes, often with branches of the rachis twisted and blanched.

In a field of Abundance oats very severely attacked by frit fly the panicles began to unfurl about the 20th June and large numbers of "blind" spikelets were noticed.

Examination of several ears still enclosed in the swollen sheath on June 24th, revealed the presence of a larva of frit fly in a number of these, feeding amongst the folded flowers. Subsequent examination of unfurled panicles made frequently until the end of July showed in many cases two or even three larvae. The intensity of the attack causing irregular ripening through the production of more tillers, coupled with the fact that plots were sown at different dates extending into May, enabled the observations to be made over this extended period. The larvae were found anywhere amongst the curled up mass of the panicle protected from the outside by the enclosing leaf and destroying completely the enclosed flowers, leaving the blanched flowerless glumes and curled branches of the rachis. In the worst cases the whole panicles were destroyed leaving only the central axis and branches which presented a blanched and twisted appearance on unfurling.

Further search on the same day, June 24th, in those cases where the first spikelets of a panicle had emerged, revealed several pupae. The pupa is fixed amongst the curled up mass, apparently anywhere—on the outside of the spikelet, rarely inside it, on the rachis or more rarely on the inside of the leaf sheathing the panicle.

It is apparently loosely attached though undoubtedly as securely as in the stem or grain attacks. When the panicle pushes out of the enclosing leaf and still more as the panicle itself expands, the pupa is almost invariably forced off and falls to the ground. Many pupae were obtained during the season still attached to the open panicles, but the proportion was very small, so that had the attack been mild or only moderately severe, it would have been very difficult to have found any at all.

An examination of the field therefore seldom gives any indication of the cause of the trouble.

Whether the imagines emerge from pupae on the ground or at the time the ears are unfurling cannot be answered definitely at present, but from the dates of hatching of those obtained one would almost conclude from the ground.

The first fly was hatched indoors on July 2nd, but the main bulk appeared later, approximately the third week in July. This period it must be understood is based on the year's observations only, and most of the specimens were gathered on an area where the dates of sowing varied from March 28th to May 13th giving therefore almost as wide a range of maturing of the crop as it is possible to get.

VARIETIES OF OATS.

The data given above were obtained on a field of Abundance oats, but examination of oat fields over many farms on a wide area fully supported them. A careful study was made of a number of oat varieties, sown on the same day (April 9th), and grown side by side, to see if variety had any effect on the intensity of the "blindness" attack.

The results are given in the table below.

Variety of oats		Percentage of ears containing "blind" spikelets	Variety of oats		Percentage of ears containing "blind" spikelets
Abundance	...	26	Golden Rain	...	58
Thousand Dollar		38	Yielder	...	56
Banner	...	47	Dunns	...	33
Victory	...	52	Welsh Grey	...	25
Supreme	...	22	Clemrothery	...	49
Record	...	31	Hero	...	20
Sandy	...	26	Crown	...	44
Potato	...	74	Blainslee	...	22
Leader	...	35	Tartar King	...	40
Black Tartarian		30	White Tartar	...	27
White Tartarian		21			

From this it will be seen that all varieties were attacked. It must be remembered that this table deals with ears only, the individual "blind" spikelets were not counted. Hence the table is no criterion of the actual damage, one variety may have had a few ears attacked severely and another a large number of ears attacked slightly.

POSITION OF THIS ATTACK IN THE LIFE CYCLE OF THE FRIT FLY.

In this country entomologists have long recognised three broods—one on grasses, one on the oat stems and another in the oat grains. There has always been a difficulty, if the broods were sharply defined, of the long interval between the tillers dying in spring and the grain being attacked. This difficulty was emphasised by Ritzema Bos as early as 1891. A brood intermediate between the one on the oat stems and the one in the grains has been somewhat uncertain in this country. The association of the name brood with the nature of attack has possibly added somewhat to the uncertainty, but more particularly the apparent overlapping of the broods is a difficulty.

The following table indicates the position of this attack in the life cycle. It is based on field observations in Shropshire extending over five years, except this particular attack, which is on one year.

Site of pupa	Earliest gathered pupa	Period of maximum emergence of flies
Grass stems (<i>Arrhenatherum</i>)	March 25th	1st week of May
Base of oat tillers	May 21st	Middle of June
Panicle inside leaf	June 24th	3rd week of July
Oat grains	July 31st	1st week of September

The period of maximum emergence is given because both stem attack and this attack causing "blindness" continue until harvest as more tillers are produced and more panicles unfurl.

This table would seem to supply evidence in the field in this country in support of dates obtained from indoor cultures by Dobrovliansky in Russia during 1915 (*vide* Collin in *Annals of Applied Biology*, vol. v, p. 85).

CONCLUSION.

From the abundance of evidence obtained last summer I feel justified in suggesting that there may be three broods of frit flies on the oat crop and that "blindness" is caused by the intermediate one. Probably only a certain percentage of the intermediate brood cause this "blindness"—the remainder entering newly forming tillers. Perhaps the scarcity of

suitable tillers, in view of the more advanced condition of the crop and the consequent lessening of the light at the base, compels a certain number to choose the next most suitable site, with the results shown.

Exact information on this matter, however, is not available.

Another site for this brood found in some abundance during 1917 was on the stems of winter wheat. The larvae were feeding on the stems from the base to at least the third node up and the pupae were found in the leaf sheath anywhere between the node and the ligule.

DESCRIPTION OF PLATE XII

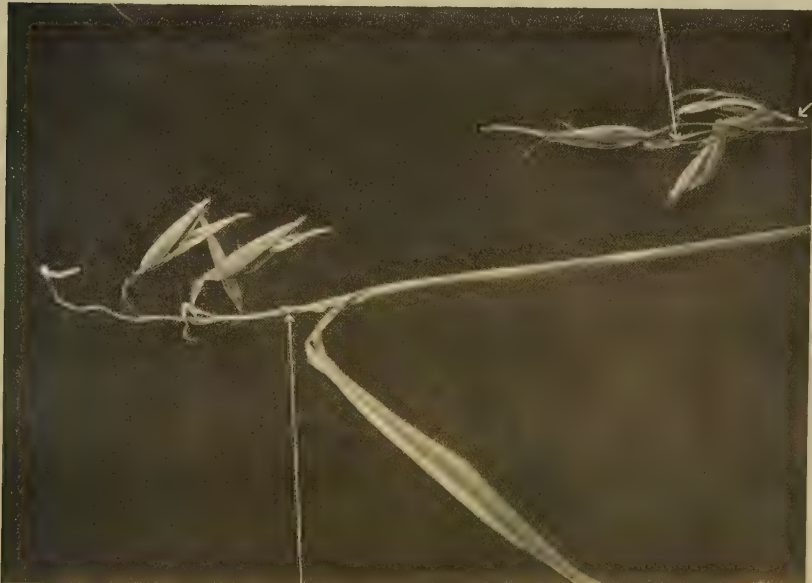
Fig. 1. Two oat ears attacked with pupae *in situ*. Higher oat ear with pupa on rachis. Lower one with one pupa in centre and one at the base.

Fig. 2. Specimens of frit fly damage on panicles. (The one in the bottom right-hand corner has lost all spikelets.)



Fig. 2.

Pupa



Pupa

Fig. 1.

Pupa

MYCOLOGICAL STUDIES. I ON THE "SPOTTING" OF APPLES IN GREAT BRITAIN

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(With 6 Text-figures.)

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1. INTRODUCTION.

THIS investigation was undertaken with a view to enquiring into the nature and origin of the spots which occur on the surface of a large number of varieties of apple, including many much prized for culinary and dessert purposes in this country; these spots, which begin to appear towards the end of the summer, spoil the appearance of the apple and are often the cause of premature decay.

This "spotting" of apples is prevalent in the United States and investigations have been undertaken or are in progress at several of the Agricultural Experimental Stations there. The earlier workers, notably L. R. Jones (Vermont)¹, Longyear (Michigan)² and Lamson (New Hampshire)³, attributed the "spotting" to various fungi, for example,

¹ Jones, L. R. *Vt. Agr. Exp. Sta. Rept.* 5 (1891), p. 133.

² Longyear, B. O. *Spec. Bull. Mich. Agr. Expt. Sta.* 25 (March, 1904).

³ Lamson, W. H. *N. H. Coll. Bulls.* Nos. 27 (Apr. 1895), 45 (May, 1897), 65 (May, 1899), 101 (Apr. 1903).

Dothidea pomigena (L. R. Jones), *Phyllachora pomigena* (Schw.) Sacc. (Longyear), but lacked the opportunity to verify their suppositions by cultural experiments.

In 1908 Charles E. Brooks¹ proved by cultural methods that *Cylindrosporium pomi*, in a later paper² identified as *Phoma pomi*, was capable of causing "spotting" in the Baldwin variety.

In 1911 W. M. Scott³ isolated *Cylindrosporium pomi* and species of *Alternaria* from the Jonathan variety, but concludes that the cause of the disease is unknown. *Alternaria* has been obtained also by M. T. Cook and G. W. Martin (1914)⁴ from large light brown spots on Jonathan apples.

Finally E. C. Stakman and R. C. Rose⁵ have announced an investigation into a fruit spot of the Wealthy apple.

Besides the fungi found during enquiries more directly concerned with the "spotting" of apples, others which generally cause rotting or twig canker have been recorded as causing "spotting," for example, *Phoma mali* Schultz. et Sacc. (Charles E. Lewis⁶), *Physalospora cydoniae* (Clinton)⁷, *Phyllosticta solitaria* (John W. Roberts⁸), and *Glomerella cingulata* (Dastur⁹).

In Britain, on the other hand, little work has been done. Towards the end of 1914, some correspondence was published in the *Gardeners' Chronicle*¹⁰ with reference to a disease of apples which was puzzling fruit growers. The apples were covered with sunken spots which often developed after the fruit was stored. The varieties affected at the time were Ecklinville Seedling, Warner's King, Cox's Pomona, James Grieve, and Rival. The disease was also developing in Peasgood's Nonsuch, Gascoigne's Scarlet Seedling, Newton Wonder, and Blenheim Pippin. Fruits of Gascoigne's Seedling remarkable for size and colour, and apparently sound early in November (1914), were at the end of the month unrecognisable through the disease. This disease was thought to be due to *Cylindrosporium pomi*; but it was pointed out that no

¹ Brooks, Charles E. *Bull. Torr. Bot. Club*, 35 (1908), p. 423.

² Brooks, Charles E. and Black, Caroline. *Phyt.* II (1912), p. 63.

³ Scott, W. M. *Phyt.* I (1911), p. 32.

⁴ Cook, M. T. and Martin, G. W. *Phyt.* III (1913), p. 119.

⁵ Stakman, E. C. and Rose, R. C. *Phyt.* IV (1914), p. 333.

⁶ Lewis, Charles E. *Maine Agr. Exp. Sta. Bull.* No. 170 (1909).

⁷ Clinton, G. P. *Connec. Agr. Exp. Sta. Rept.* Part V (1905), p. 264.

⁸ Roberts, John W. *U.S.A. Dept. Agr. Bur. Pl. Ind. Bull.* 534 (1917), p. 1.

⁹ Dastur, J. F. *Ann. App. Biol.* VI (1920), p. 262.

¹⁰ "A Southern Grower." *Gard. Chron.* No. 1457 (Nov. 28, 1914), p. 357; Cornish, P. E., *l.c.* p. 357.

English mycologist appeared to have given any considerable attention to the subject, and that it was very important that mycologists in this country should be able to inform growers to which malady, whether bitter pit or *Cylindrosporium* spot, any attack was due.

These considerations furnished the incentive to study the "spotting" problem. Early in the following year we received reports from Kent, Surrey and Berkshire of "spotting" in other varieties, notably in Bramley's Seedling, Cox's Orange Pippin and Allington Pippin, and specimens were forwarded for examination by several fruit growers. It was reported from Kent that very many of the finest and best ripened apples had become covered with very small red spots: this had not prevented the apples from keeping, but it had greatly injured their sale. The trouble developed entirely in apples in store. Barker¹ reported "spotting" in Allington Pippin and Bramley's Seedling from Worcestershire, Cambridgeshire, Oxfordshire and Sussex, and concluded that the trouble was general throughout apple growing districts.

2. SYMPTOMS.

The spots show considerable variety in form and colour. They are sometimes green, of a darker shade than the normal skin colour, as for example in Lord Derby, Newton Wonder, and Reinette du Canada, where dark green blotches show up conspicuously on a yellow-green skin. In the case of a pigmented apple, the spots are usually of a darker shade of red or purple than the normal (Scarlet Nonpareil). In varieties with partial pigmentation, the spots are frequently coloured rose, red or purple (Mrs Philimore, purple spots on a green ground); coloured spots also appear in normally unpigmented varieties such as Old Nonpareil, Reinette du Canada (blotches with purple edging), and Lane's Prince Albert (dark brown blotches bordered pinkish red).

Curiously mottled blotches are sometimes formed with the mottlings in purple, purplish brown and green; for example, Ribston Pippin, Old Nonpareil, Cox's Orange Pippin, Charles Ross (brown, and purplish brown).

Dark brown spots occur in Ecklinville Seedling, Yorkshire Greening, etc.; pale brown spots in Cox's Orange Pippin, Charles Ross, Emperor Alexander, Peasgood's Nonsuch (spots with irregular contour), and Duke of Devonshire. In Hollandbury the spots are dark, of irregular outline, angular and so numerous as to give the apple a fantastic appearance. The

¹ Barker, B. T. P. *Ann. Rept. Agr. and Hort. Res. Sta., Long Ashton* (1914), pp. 97-99.

dark brown, slightly sunken spots in Wellington resemble a scurf; in Tamplin they are often round, sunken, numerous and very small.

Minute black markings of various kinds are frequently present in the brown spots which add a great variety of minute detail. The spot may be almost uniformly black (September Beauty, Rev. W. Wilks, Early River, Wolf River), or black dendritic markings may appear (Newton Wonder). These appearances are due to the presence of fungi with dusky mycelium, for example, *Alternaria*, *Dematium pullulans*, etc. Again, the spot may be dotted in various patterns with the dark sclerotial or other reproductive bodies of various fungi, and the pattern will vary with the kind and degree of development each has attained. The following fungi have been found to produce this "dotted" effect:



Fig. 1. Photographic reproduction showing mummification following "spotting" of apples.

- (1) *Pleospora pomorum*—black sterile perithecia.
- (2) *Valsa* sp.—necks of the perithecia.
- (3) *Polyopeus purpureus*—dark brown pycnidia (Early River, Stirling Castle).
- (4) *Myxosporium mali*—black sclerotial bodies.
- (5) An unidentified fungus with thick glistening walls—black sclerotia.

Perithecia often escape recognition since only a portion of the perithecium (*Pleospora*), or only the extremity of the neck (*Valsa*) protrudes above the surface of the apple.

It is not meant to be understood that the spots named are necessarily of different origin; a purple spot and a brown may differ in aspect merely

through varietal characteristics of the apples on which they occur: conversely, spots of a somewhat similar category—brown spots, for example—should not be held to indicate a likeness of origin, since a brown colour is one of the commonest symptoms of a pathological condition.

Spots of different kinds may occur on the same variety and even on the same apple. There were on Lane's Prince Albert, received from Berkshire at the end of April, 1915, pale brown spots with a dark brown centre; chocolate brown spots with a pale centre, and blackish spots mottled with green; some spots were variously dotted, others not. On other apples of this variety received at the same time, dendritic markings were present on a pale brown ground, and in the same variety greenish and purplish sunken blotches and dark brown spots with a pinkish red border also occur.

"Spotting" has been observed in about one hundred varieties of apple, and occurs in a widely representative series of varieties—early, mid-season and late, and whether culinary, dessert or exhibition—including a number of sorts most prized in commerce. The varieties which escape include hard-fleshed apples, notably the russets (Christmas Pearmain, Worcester Pearmain, etc., with the exception of Hubbard's Pearmain): the late pippins (Allen's Everlasting—a seedling from Sturmer Pippin, Fearn's Pippin, etc.); also, as far as observations of 1917–18 show, certain other varieties with crisp sub-acid flesh, such as Barnack Beauty, Gloria Mundi, Belle Dubois.

"Spotting" in relation to the lenticels.

The surface of the apple is studded with numerous minute pale, more or less stellate, apertures which are more conspicuous on some varieties than others. These are usually referred to as lenticels¹, although they do not possess the typical structure of such organs. McAlpine² states that they are formed through rupture of the stomata as a result of expansion as the apple increases in girth; he gives a photographic reproduction of a pore showing the remains of a stoma (McAlpine, Plate XIV, fig. 102). They take their origin therefore in the same way as lenticels.

In a number of cases the spots originate at the lenticels. A careful examination will show a complete series of stages from discoloured lenticels to spots. In Wellington the smallest spots just encircle the

¹ The stomata are not all ruptured by the time the apple reaches maturity: stomata were observed quite late in the season in a large specimen of an unknown variety.

² McAlpine. "Bitter Pit Investigation," *First Progress Report* (1911–12), p. 40.

lenticel, and there are others of every intermediate stage between these and the largest in the apple. In Ecklinville Seedling nearly every lenticel in the apple is brown and in a large number of them brownness has spread round to form a spot varying from the size of the lenticel itself to one-eighth of an inch in diameter. On Stirling Castle with dark spots the lenticels show up conspicuously brown. On Golden Spire there are dark brown spots on one apple and pale brown on another, the size of a pin's head. On Lane's Prince Albert received in December 1915 from Berkshire, the smallest spots were of the same dimension as the lenticels.

These observations confirm those of Charles Brooks¹, Barker², Cook and Martin³ and others as to the importance of the lenticel in relation to incipient "spotting"; but the lenticels are not the only centres of origin, since the opportunity for infection occurs wherever stomata exist or where the skin is injured by cracks or wounds of any kind.

Development of "spotting."

"Spotting" usually appears towards the end of July, and there is a considerable development in August. On September 29th, 1915, "spotting" was observed on 31 varieties at Wisley. The production of new spots goes on continuously throughout the storage period until the coming of spring: over 200 spots were counted on a specimen received from Sussex in 1915.

The progress of "spotting" was specially studied in a collection of over ninety varieties of apples at the Royal Horticultural Society's Gardens in 1917-18, from two to four specimens of each variety being examined. Of these, 30 varieties remained free during the season. In some kinds spots developed early in the season and remained without further development; for example, in King of Tomkins County (seasonal period September-April), depressed blackish brown spots up to $\frac{1}{4}$ in. diameter were present early in November, but remained with little increase in size until May. In others, there was a steady increase in size; thus in Ribston Pippin (November-January) numerous minute brown spots were present early in November: these increased to $\frac{1}{8}$ in. (November 22nd) and $\frac{1}{4}$ in. in diameter (November 28th); soon afterwards the apples became rotten. In Yorkshire Greening (October-January), there were few depressed brown spots and brown spots with

¹ Brooks, Charles E. *Bull. Torr. Bot. Club.* 35 (1908), p. 423.

² Barker, B. T. P. *Ann. Rept. Agr. and Hort. Res. Sta., Long Ashton* (1914), p. 98.

³ Cooke, M. T. and Martin, G. W. *Phyt. l.c.*

a black centre up to $\frac{1}{4}$ in. in diameter; these remained arrested until January 31st, when the largest spot was 1 in. in diameter; the apple then rotted. In over 20 varieties, rotting which could be traced to "spotting" had set in before the varieties were out of season.

3. THE FUNGI CONCERNED.

Owing to the fact that so few of the black bodies found in "spot" areas proved fertile, cultural methods were adopted in the hope that reproductive bodies which would facilitate the work of identification, would be formed in the media employed.

The apple was first washed in .1 per cent. mercuric chloride solution, and then rinsed thoroughly in sterile water: small cubes from 1-5 mm. long were cut out rapidly with a sterile knife and dropped into apple extract or on the surface of apple agar—in some cases the cubes were immersed for a few seconds in mercuric chloride followed by washing in sterile water before they were transferred to the medium. Control cubes were taken from unspotted parts of the apple and invariably gave negative results. Cubes taken from bitter pit areas also yielded negative results.

The first fungi were isolated in the autumn of 1915, but owing to circumstances a number of cultures were abandoned and only those considered to be of importance at the time were carried on. Further work was started in the autumn and winter 1917-18 and another series of cultures obtained: these included all the fungi carried on from 1915, with the exception of species of *Alternaria* and *Sclerotium*, and in addition a number of others which were not obtained in the first period.

The total number of isolations in both periods exceeds 400: of these, 140 were in the first period and 260 in the second. The actual number of failures to isolate fungi in the first period exceeded 50 per cent., due in some cases to the use of liquid apple extract, and in others to over-sterilising in mercuric chloride the inoculation cubes. In the second period out of 38 placed in extract, 19 failed—exactly 50 per cent., whereas of those placed on apple agar only seven failed, being cubes obtained from four varieties of apple.

The fungi present in the original cultures were separated by plating out or by transference to slant tubes; in this way several fungi whose identity could be determined were obtained in pure culture; and notably *Leptosphaeria vagabunda* Sacc., *Coryneum foliicolum* Fuck, *Fusarium*

*mali*¹ Allersch., *Myxosporium mali*² Bresadola and *Alternaria grossulariae* Jacz³.

Others whose identity could not be determined were regarded as separate fungi from the fact that the general characteristics remained fairly constant in successive sub-cultures. They were transferred to potato mush agar in the autumn of 1918 and in the majority of cases reproductive bodies were formed. These fungi⁴ include:

(a) Species of a phomoid genus differing from *Phoma* in possessing compound, unilocular pycnidia with multiple necks, to which the name *Polyopeus*⁵ is given—*P. purpureus*, *P. pomi*, *P. recurvatus* and *P. aureus*.

(b) An aggregate species of *Fuckelia*—*F. botryoidea*.

(c) A species of *Coniothyrium* with lobed pycnidia—*C. convolutum*, and a form of *C. cydoniae*.

(d) A species of *Alternaria* forming in media "pockets" of conidia—*A. pomicola*.

(e) A species of *Pleospora*—*P. pomorum*, with a dematiaceous stage of the *Stemphylium pyriforme* type. The identity of the conidial and ascigerous stages has been proved by reciprocal single spore cultures.

(f) A species of *Sclerotium*—*S. stellatum*, somewhat resembling *S. bataticolum*⁶.

Three other fungi have not yet formed reproductive bodies rendering identification impossible; they are:

(a) The thick-walled fungus to which reference has been made.

(b) A slow-growing fungus presenting a dingy white and somewhat powdery appearance at the surface of the medium when grown on apple agar. This fungus was obtained 21 times from spots, with a centrally situated lenticel, varying in size from $\frac{1}{16}$ to $\frac{1}{8}$ in. in diameter.

(c) A sterile fungus, isolated from Ben's Red and King of Tomkins County, producing brilliant colours when grown on different media. On apple agar the colours vary from dull pink to bright orange-yellow; on potato slants they vary from pink to yellow, yellow-green with a

¹ See Allescher. *Ber. Bot. Ver. Landshut.* XII, p. 130 (1892); and Oudemans, *Cat. Champ. Pays Bas*, p. 531.

² See Bresadola. *Hedwigia*, p. 382 (1897).

³ This apple *Alternaria* proved morphologically identical with *Alternaria grossulariae* (Jaczewsky, *Bull. Soc. Myc. Fr.* XXII, 1906, p. 122), isolated by one of us from gooseberries.

⁴ For descriptions of the new species see the *Journal of Botany*, vol. LVIII, p. 239. (Oct. 1920).

⁵ The morphological and physiological characteristics of this genus will be described elsewhere.

⁶ Tubenhaus, J. J. *Phyt.* III (1913), p. 164; also Martin, William H. *Phyt.* VII (1917), p. 308.

metallic lustre and orange, and on potato agar plates bright shades of green and blue have appeared.

The effect produced by these various fungi in the tissues of the apple can only be outlined in very general terms. In sections through a small spot, where of course there may be one fungus or two or more associated fungi, the mycelium is present in the air spaces: the hyphae penetrate between the cells and envelop them in a web of filaments firmly adhering to the cell wall. The cells lose their hyaline character through changes in the protoplasm and plastids, and become brown—the tissue is darker when fungi with dusky mycelium are present. In some cases mycelium is present in a hyaline zone in advance of the discoloured region.

SPECIAL RELATIONS OF THE FUNGI CONCERNED IN "SPOTTING."

The fungi isolated from the smallest spots ($\frac{1}{16}$ – $\frac{1}{8}$ in. diam.) include *Pleospora pomorum*¹, *Leptosphaeria vagabunda*, *Polyopeus purpureus*, *P. pomi*, *P. recurvatus*, *P. aureus*, *Fuckelia botryoidea*, *Coniothyrium convolutum*, *Alternaria grossulariae*, *Coryneum foliicolum*, *Myxosporium mali* and certain unidentified forms. Among these fungi are to be sought those responsible for the commencement of "spotting."

In the majority of cases small spots have yielded only one fungus, for example *Alternaria grossulariae* (Ben's Red); *Polyopeus purpureus* (Byford Wonder, Charles Ross, Bismarck). But spots of this category even when occurring on the same apple have not always yielded the same fungus, for example, the brown spots on Margil yielded *Polyopeus aureus*; the dark brown spots, *Fuckelia botryoidea*; again the pale brown spots on Frogmore Prolific yielded *Fuckelia botryoidea*; other spots, *Leptosphaeria vagabunda*. On September Beauty two spots yielded *Alternaria grossulariae* and two *Polyopeus purpureus*. *Alternaria* and *Polyopeus* spots occur also on Wolf River and Grenadier.

In some cases two or more fungi may be associated in small spots; for example, *Alternaria grossulariae*, *Polyopeus purpureus* and an unidentified fungus, in Byford Wonder. Here we have two fungi associated which in the same variety also occur singly in spots. In a spot on the variety Rev. Wilks, somewhat larger than those above mentioned, certain spots yield only *Alternaria grossulariae*, but other spots on the same apple yield the same fungus in association with *Myxosporium mali*.

¹ For the apple varieties from which *Pleospora pomorum* and other fungi have been isolated, see *Journal of Botany, l.c.* and *The Gardeners' Chronicle*, vol. LXVIII, October 30, 1920, p. 216.

As regards the frequency with which a particular fungus occurs alone in spots, data can only be given for *Pleospora pomorum* and fungus *b*; the former was found unassociated in eight out of nine varieties studied (in the ninth case *Polyopeus purpureus* was present in addition); in the latter, in 12 out of 15.

Taking into account the total number of spots of all categories, *Pleospora pomorum*¹ has been isolated from 18, *Polyopeus purpureus* from 20 varieties. Only six of these varieties yielded both fungi. *Alternaria grossulariae* occurred in seven varieties of which two (Byford Wonder and Ben's Red) also yielded *Pleospora*, and four (Early River, Grenadier, Rev. W. Wilks, and September Beauty) *Polyopeus purpureus*.

The apples from which *Pleospora pomorum* has been isolated are by no means of a similar class; they include dessert (Cox's Orange, Ben's Red), culinary and dessert (Bramley's Seedling, Wealthy), and culinary (Byford Wonder) sorts; also varieties in season in late autumn (Loddington), and in winter (King of Tomkins County). *Polyopeus purpureus* occurs also in both culinary and dessert varieties, and notably in the culinary varieties Newton Wonder and Lane's Prince Albert, varieties with a wide seasonal range, but it also occurs in varieties with a restricted range as Grenadier.

Fungus *b* has been isolated from dessert and culinary sorts—Alfriston (Nov.-Apl.), Lord Hindlip (Jan.-May), Belle de Pontoise (Dec.-Feb.), Duke of Devonshire (Mar.-Apl.), etc.—chiefly from apples in season after November.

The surface spots present on apples badly affected with “bitter pit” frequently yielded fungi; for example, on Newton Wonder some spots yielded *Cladosporium epiphyllum*, others *Dematium pullulans* and fungus *b*, others slow-growing unidentified fungi (minute dark brown spots). Fungi were not obtained from “spotted” specimens of Calville Boisbunel, Crawley Beauty, Sanspareil and Yorkshire Greening.

The largest spot-flora has been obtained from Cox's Orange Pippin—eight species excluding unnamed fungi: two fungi were obtained from Blenheim Orange, fungus *b* from small spots and later *Myxosporium mali*² from areas where rot had set in.

Of the important culinary varieties, Lane's Prince Albert yielded *Dematium pullulans* four times, *Polyopeus purpureus*, *recurvatus*, and

¹ The earliest date on which it has been obtained is Nov. 15th (Charles Ross), and the latest, early in March (Bismarck).

² Also isolated from Byford Wonder, Domino, Duke of Devonshire, Lord Grosvenor, Lord Suffield, Rev. W. Wilks, Winter Hawthornden.

Cephalothecium roseum; Newton Wonder, *Polyopeus purpureus*, fungus b four times and *Cladosporium epiphyllum* twice; Potts's Seedling, *Polyopeus purpureus*, *Cladosporium epiphyllum*, *Fusarium mali*, and unidentified fungi; Ecklinville Seedling, *Dematium pullulans*¹ and fungus b; Bramley's Seedling, *Pleospora pomorum*, *Cladosporium epiphyllum*² and unidentified fungi; Peasgood's Nonsuch, unidentified fungi (reddish brown spots).

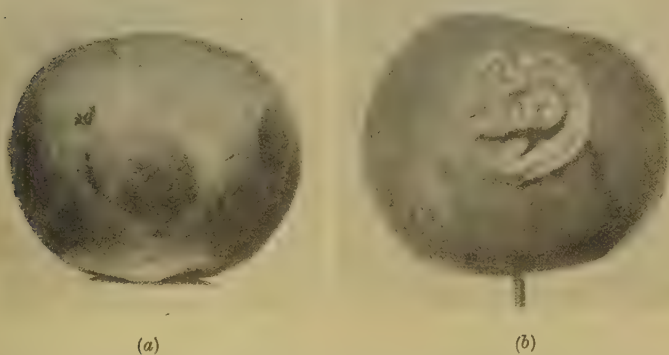


Fig. 2 (a). Photographic reproduction of an apple inoculated with conidia of *Pleospora* at two points, after seven weeks, showing infertile perithecia (see Fig. 3 a for representation of the same apple after two weeks).
(b) Photographic representation of an apple inoculated with conidia of *Pleospora* at four points, after seven weeks (see Fig. 3 d for a diagrammatic representation of the same apple).

5. INOCULATIONS WITH *PLEOSPORA*³ *POMORUM* HORNE.

On Jan. 17th, 1917, an apple of unknown variety was inoculated at four points by introducing, through punctures made with a sterile needle, fragments of mycelium bearing conidia (*Stemphylium*) of *Pleospora pomorum*. Five days afterwards, spots were observed at the points of inoculation. On Feb. 22nd, large dark brown areas had developed, and the apple was rotting. Since other spots had formed at points not inoculated another sound apple was inoculated on Jan. 17th, and a number of

¹ Also isolated from Allington Pippin, Christie Manson, Crawley Beauty, Lord Suffield, Tamplin, Scarlet Nonpareil, Stirling Castle.

² Also isolated from small spots in association with other fungi in Christie Manson, Landsburger Reinette, Lord Suffield, Tamplin and Winter Quarrenden.

³ A full account of the reactions to various media is omitted for reasons of space.

control punctures were made on a third apple. On Feb. 22nd, brown spots $\frac{1}{4}$ in. diameter were observed, but again spots appeared at places not inoculated. However, on Feb. 28th, the four spots formed at the points of inoculation on this apple had coalesced to form an area 1 in. in diameter. The apple was then cut open and portions of diseased tissue were removed from the interior at a depth of $\frac{1}{2}$ in. from the surface.

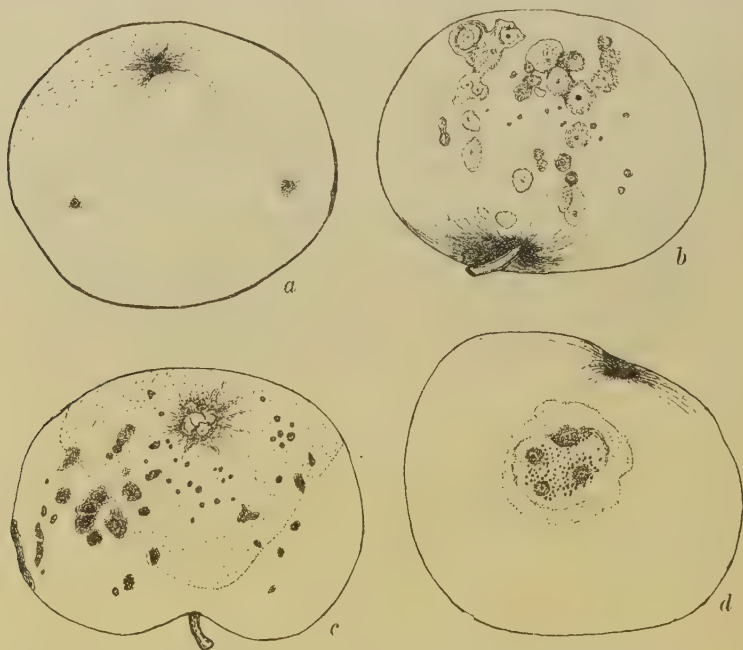


Fig. 3 (a). Apple inoculated with conidia of *Pleospora* at two points, after two weeks (see Fig. 2 a for photographic reproduction of the same apple after seven weeks).

(b) Apple affected with "spotting," March, 1915.

(c) Apple showing rot (shaded portion) following "spotting."

(d) Apple inoculated with conidia of *Pleospora* at four points, after seven weeks, showing infertile perithecia (see Fig. 2 b for a photographic reproduction of the same apple).

Some portions were placed in sterile petri dishes and others on the surface of apple agar in slant tubes. After a few days abundant conidia and later sterile perithecia of *Pleospora* were formed in both dishes and tubes.

Experiments were then made with known varieties. Specimens of Lane's Prince Albert and Newton Wonder were inoculated on March 14th. In the case of Lane's Prince Albert a spot about $\frac{3}{8}$ in. in diameter was present on April 3rd, increasing to a pale brown area with dark centre

1½ ins. in diameter on April 11th and 2¼ ins. in diameter on April 23rd; in the case of Newton Wonder, small spots ⅓ in. in diameter were present on April 11th which increased to ½ in. on April 23rd. In both cases black, sterile perithecia of *Pleospora* developed in the diseased areas.

A number of apples were inoculated with *Pleospora pomorum* while still on the tree in August, 1917. A representative series of varieties was chosen including two varieties, viz. Bismarck and Charles Ross, from which this fungus had been isolated.

The method adopted was as follows: two spot-free apples were chosen of each variety and punctures made (using a sterile needle) in each; one apple was inoculated with a minute fragment of mycelium bearing conidia, and the other not inoculated. After inoculation the apples were enclosed in manilla bags similar to those used in pollination experiments. The apples, by design, were not sterilised before inoculation, as it was desired not to injure the surface of the apple in any way. The inoculant was therefore exposed to competition from fungi already present on the apple. Records of the appearance, etc., were taken at short intervals. As the apples ripened they were removed from the tree and stored under suitable conditions.

Of the 28 varieties inoculated, spots were not formed at the point of inoculation in five, viz. the firm-fleshed russet—Court Pender Platt, Norfolk Beaufin¹, Charles Ross², Ribston Pippin and Cellini. Small spots were formed which remained arrested for a period in seven varieties, of which five are culinary sorts—Alfriston, Allen's Everlasting, Beauty of Kent, Calville Boisbunel, Cockle's Pippin, King of the Pippins and Lord Derby. The remaining 16 varieties developed "spotting" more or less rapidly and rotting ensued—Allington Pippin, Belle de Pontoise, Bismarck, Bramley's Seedling, Cardinal, Crawley Beauty, Duchess Favourite, Early Victoria, Grenadier, Keswick Codling, Lane's Prince Albert, Potts's Seedling, Red Astrachan, Rival, Royal Jubilee and Wealthy.

In the case of five of the 16 varieties which eventually rotted—Allington Pippin (Jan 11th), Rival (Jan. 11th), Wealthy (Dec. 31st), Royal Jubilee and Cardinal—*Pleospora* was re-isolated from the diseased tissue. In the first four of these the development of spotting occurred between Sept. 12th and the end of November, that is approximately the time these varieties are in season. In the early variety, Cardinal,

¹ Large natural spots formed on the inoculated apples.

² The failure to infect Charles Ross is noteworthy, since *Pleospora* was isolated from this variety on Oct. 25th, 1915.

rotting took place earlier. A sound Cardinal apple placed in contact with the diseased specimen rotted within a month.

In the case of the varieties Rival, Wealthy, and Allington Pippin, no fungus other than *Pleospora* was isolated from the rotting areas which developed in the apples inoculated with *Pleospora*.

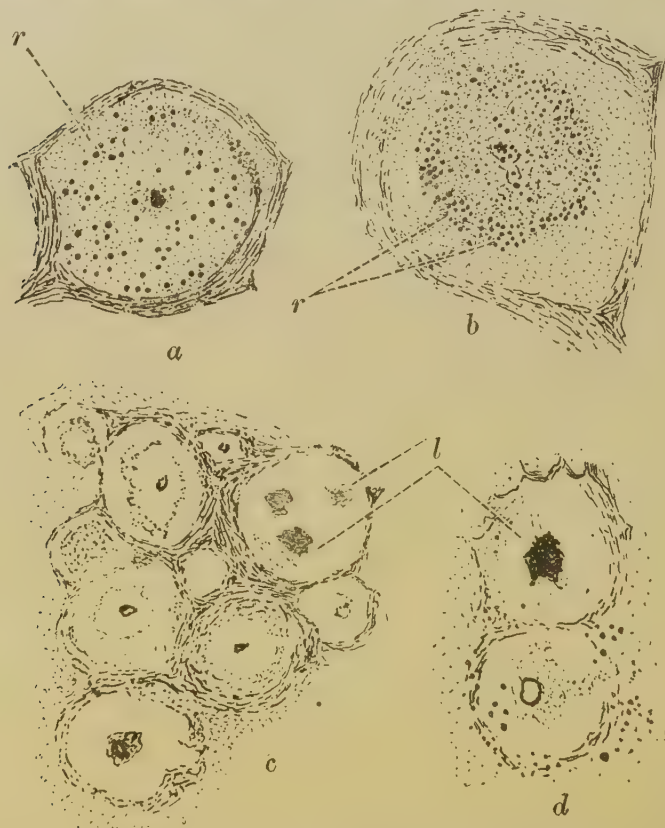


Fig. 4 (a-b). "Spots" on surface of apple enlarged showing black reproductive bodies of fungi (r). (c-d). Group of "spots" enlarged showing lenticels (l).

In the case of the Cardinal apple, however, the presence of a second fungus, *Polyopeus purpureus*, in the diseased tissue was revealed from re-isolation tests made after Sept. 13th. On the following day cubes from the diseased portions in which *Pleospora* mycelium was present were placed in petri dishes in a moist atmosphere. The mycelium which

developed was carried on in plate culture and eventually yielded either *Pleospora* or *Polyopeus purpureus*, or both. On Sept. 20th, some more



Fig. 5. Conidial stage of *Pleospora pomorum* (*Stemphylium*).

(a) Portion of conidiophore.

(b) Sporophore showing swollen end-cells (e) and mature conidia (c).

cubes were cut and dropped on the surface of apple agar in slant tubes. On this occasion abundant conidia (*Stemphylium*) were produced within four days, but no *Polyopeus*. On Sept. 26th masses of white mycelium

appeared at the surface of the apple: two tubes of agar were inoculated and yielded on Oct. 2nd, *Pleospora* and *Polyopeus purpureus* respectively.

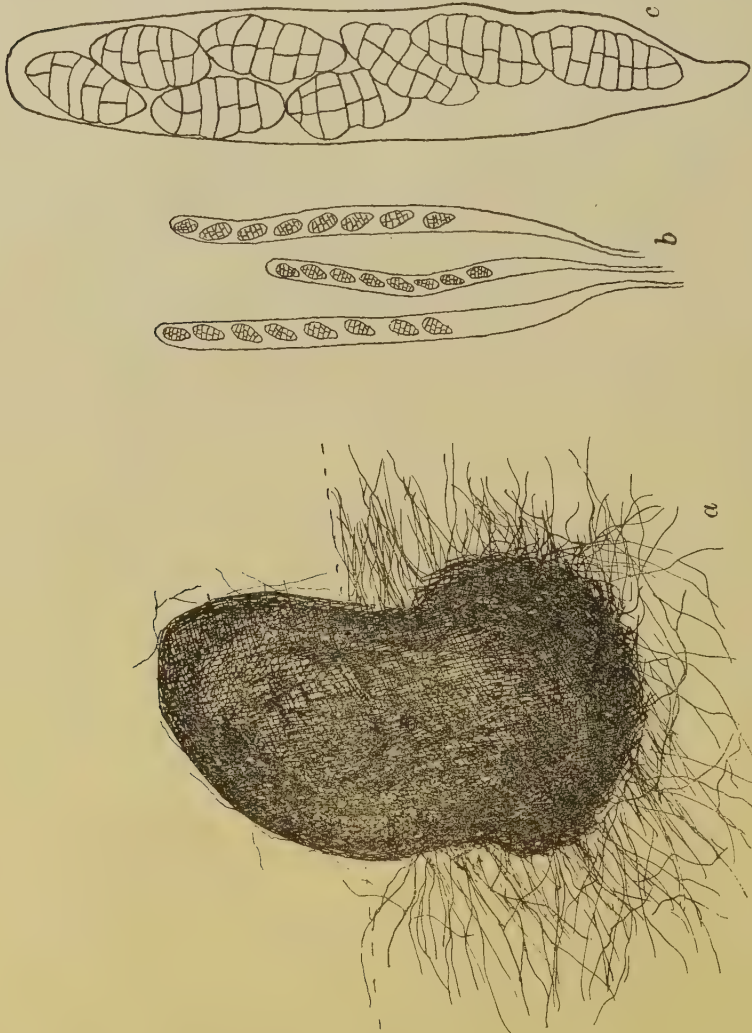


Fig. 6. Ascigerous stage of *Pleospora pomorum*.

(a) Perithecium. (b) Asci with spores in a single rank. (c) Ascus with spores in a double rank.

In Potts's Seedling (Sept.-Oct.), the diseased tissue obtained from artificially produced spots repeatedly yielded *Polyopeus purpureus* and not *Pleospora*. A spot which appeared naturally on the same apple also

yielded *Polyopeus purpureus*, but with *Fusarium mali* in addition. Another natural spot yielded an unidentified fungus. In this variety, *Pleospora* has made no progress, but a different fungus, *Polyopeus purpureus*, occurring in the natural spots on the same apple, has effected an entry¹ at the points where *Pleospora* was introduced. Again *Pleospora* was not re-isolated from Lane's Prince Albert, a variety with a wider seasonal range (Oct.-Mar.), but *Polyopeus purpureus* and another phomoid fungus were obtained instead from the artificially produced spots.

The results obtained in Grenadier (Sept.-Oct.) were somewhat different. Small brown spots appeared at the point of inoculation on Sept. 12th. These measured 3 mm. in diameter on Sept. 24th. On this date other spots were forming at the lenticels near the point of inoculation. A month later the original spots formed merely the nucleus of brown areas; in fact the apple was in a semi-rotten condition. On Nov. 8th fragments of tissue removed with sterile instruments from the diseased area near the original point of inoculation were placed on the surface of apple agar in slant tubes. After a few days *Polyopeus purpureus* and *Alternaria grossulariae* were present in the cultures. Cultures made in the same way but using tissue taken 2 ins. from the point of inoculation yielded *Alternaria grossulariae*. Finally, cultures made using eruptive mycelium taken from pustules appearing at the surface of the apple (Oct. 29th) yielded *Polyopeus purpureus*. *Pleospora pomorum* was not obtained at all, but instead two other fungi—*Polyopeus purpureus* and *Alternaria grossulariae*—which were not present in the inoculant.

6. CONTROL.

Susceptibility and Immunity.

This work has shown (Section 5) that *Pleospora pomorum* can parasitise at least three varieties of apple (Rival, Wealthy, Allington Pippin), whilst in certain other varieties (Cardinal, Grenadier, Potts's Seedling), originally inoculated with *Pleospora*, *Pleospora* was either not re-isolated (*Polyopeus purpureus* was obtained instead) or was re-isolated in association with other fungi (*Polyopeus purpureus*, *Alternaria grossulariae*, etc.). Considering together the observations noted in Section 4 and the facts recorded in Section 5, the evidence seems to suggest that both *Pleospora pomorum* and *Polyopeus purpureus* exhibit a preference for varieties,

¹ It is interesting to note in Norfolk Beaufin (Oct.-Dec.) artificially made punctures were not inoculated by the fungus or fungi causing the natural spots formed in October on the inoculated specimen.

but that the varieties preferred by the one are not necessarily those preferred by the other. But the varieties Rival, Wealthy and Allington Pippin, in season from October to December inclusive, were inoculated when unripe whereas Cardinal, Grenadier and Potts's Seedling, in season from August to October inclusive, were inoculated when ripe. Hence the inoculations in the two cases are not strictly comparable since the varieties were not inoculated at the same phase of apple development. The supposition that *Pleospora pomorum* and *Polyopeus purpureus* each exhibit a preference for varieties, for example Rival and Cardinal respectively, is therefore open to the objection that a given variety may be susceptible to one fungus at an early stage of its development and to another at a later stage; in fact, there may be a definite fungal succession. Questions of this kind can only be settled conclusively by carrying out, throughout the season, continuous comparative series of inoculations on specially selected varieties. Certain subsidiary phenomena for example, "arrested spotting" and recrudescence of "spotting" after a period of rest, would then be better understood. Considerable help would be afforded by a parallel study of the seasonal chemical changes taking place in the varieties selected for experimental purposes.

Outdoor measures.

The risks of summer infection could be considerably reduced by spraying with Burgundy mixture when the fruit is young. Very probably a weak solution thoroughly applied, similar to that successfully used at Wisley by the authors¹ to prevent the infection of gooseberries by the American gooseberry mildew, would serve the purpose. The treatment should be repeated each year, for until the life-histories of the fungi concerned in "spotting" and the various sources of summer infection are completely known, it is impossible to take comprehensive measures against seasonal recurrence. The success of spraying as a means of control has been repeatedly demonstrated in America by Lamson² and others.

Indoor measures.

Summer spraying should practically prevent the appearance of "spotting" in store unless the fungi exist in the fruit-room itself. Where no spraying has been practised, the development of "spotting" could

¹ Horne, Arthur S., in *The Gardeners' Chronicle*, LIX, p. 310 (June 10, 1916); and Horne, Eleanor V., in *The Garden*, LXXXI, No. 2374, 174 (May 19, 1917).

² Lamson, W. H. *N. H. Coll. Bulls.* Nos. 27 (Apr. 1895), 45 (May, 1897), 65 (May, 1899), 101 (Apr. 1903).

be retarded by storing at lower temperatures than those frequently adopted. It is however eminently desirable to systematically disinfect the fruit-room since some of the fungi enumerated in this paper can grow slowly and even sporulate at a comparatively low temperature (0° – 5° C.).

7. SUMMARY.

This paper presents the results so far obtained in an investigation, which has been carried on since 1915, into "spotting" in apples. The symptoms of "spotting" as they are found and develop in numerous varieties of apple are described. Several fungi have been isolated from spots and cultured in various artificial media with the production of spores.

They include a new genus of Phomatales (*Polyopeus*) and nine new species, of which at least one, *Pleospora pomorum*, as the result of experimental inoculations, has been proved capable of parasitising apples. The fungi do not include any of the species hitherto reported as causal organisms in the United States, the only centre where investigations into the "spotting" of apples, as distinct from the "bitter pit" problem, has been undertaken.

The work was commenced at the Wisley Gardens of the Royal Horticultural Society. During the building of the Society's laboratory it was continued, by the kindness of Professor V. H. Blackman, in the Department of Plant Physiology and Pathology at the Imperial College of Science and Technology. It was later carried on again at Wisley; the work however has been completed at the Imperial College.

The authors' thanks are due to Professor Blackman for his kind help and criticism during the investigation.

A QUANTITATIVE ANALYSIS OF PLANT GROWTH

PART II.

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(With 6 text-figures.)

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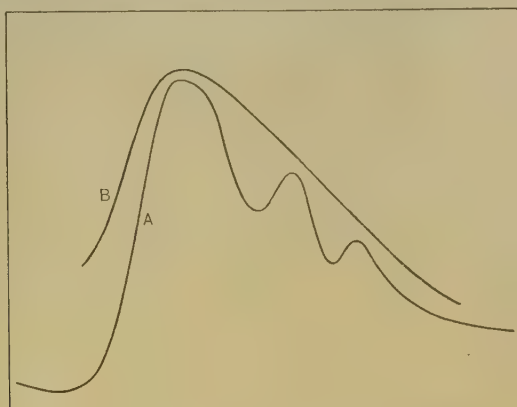
CHAPTER II.

I. UNIT LEAF RATE.

In the previous chapter we showed that the Relative Growth Rate curve, that is, the weekly percentage increase in dry-weight plotted against time, for such a plant as maize, has the general form shown in Fig. 1, curve A. Secondly, it was found that the Leaf-Area Ratio curve, that is, the leaf-area per unit dry-weight plotted against time, has the same general form, Fig. 1, curve B. This similarity in the form of the two curves suggests that the weekly increase in dry-weight per unit leaf-area is more or less constant throughout the life-cycle of the plant. In order to ascertain how far this is true we have dealt with the results of Kreusler (13, 14, 15, 16), which were quoted at length in the previous chapter (5), by calculating the values for what we propose to call the Unit Leaf Rate and presenting them for the complete life-cycle of the plant in Unit Leaf Rate curves (Tables I—IV and Figs. 3–6). The Unit Leaf Rate in this paper is the increase in dry-weight per square centi-

metre of leaf per week, taking as the leaf-area the average of the areas at the beginning and at the end of the week¹.

Before studying these values for Unit Leaf Rate in detail let us consider the possible ideal forms of the Unit Leaf Rate curve. Neglecting the possible effects of environmental factors, if no change occurs in the values of the assimilation and respiration per unit leaf-area the Unit Leaf Rate curve will be a line parallel to the time axis. With regard to assimilation, the activity of the leaves is by no means uniform. The



A. Growth-Rate Curve. B. Leaf-Area Ratio Curve.

Fig. 1.

activity of the seedling leaves is smaller than that of the more mature leaves whether carbon dioxide, light, or temperature be limiting, a conclusion which we drew as the result of the analysis of Kreuzler's data in the previous chapter, and which has been demonstrated experimentally for some plants by Irving⁽¹⁰⁾ and by Briggs⁽⁴⁾². This change in the

¹ In the appendix to this paper we have put forward two methods of calculating Unit Leaf Rate. Except during the first few weeks it is immaterial which method of calculation is used. During this early period the increase in leaf-area is most probably intermediate between linear and exponential, as an inspection of the figures for leaf-area indicate, and consequently the actual values of the Unit Leaf Rate are intermediate between those calculated by the two methods. The conclusions drawn in this paper are not affected by the method of calculating Unit Leaf Rate, and hence the simpler method is used. The values for Unit Leaf Rate for the year 1877 run as follows: 6.9, 5.6, 5.1, 3.2, 5.8 on the exponential basis and 6.1, 5.1, 4.9, 3.1, 5.7 on the linear basis.

² The question of changes in assimilatory activity of the leaf throughout its development, and of young leaves throughout the development of the plant requires more thorough investigation than it has at present received.

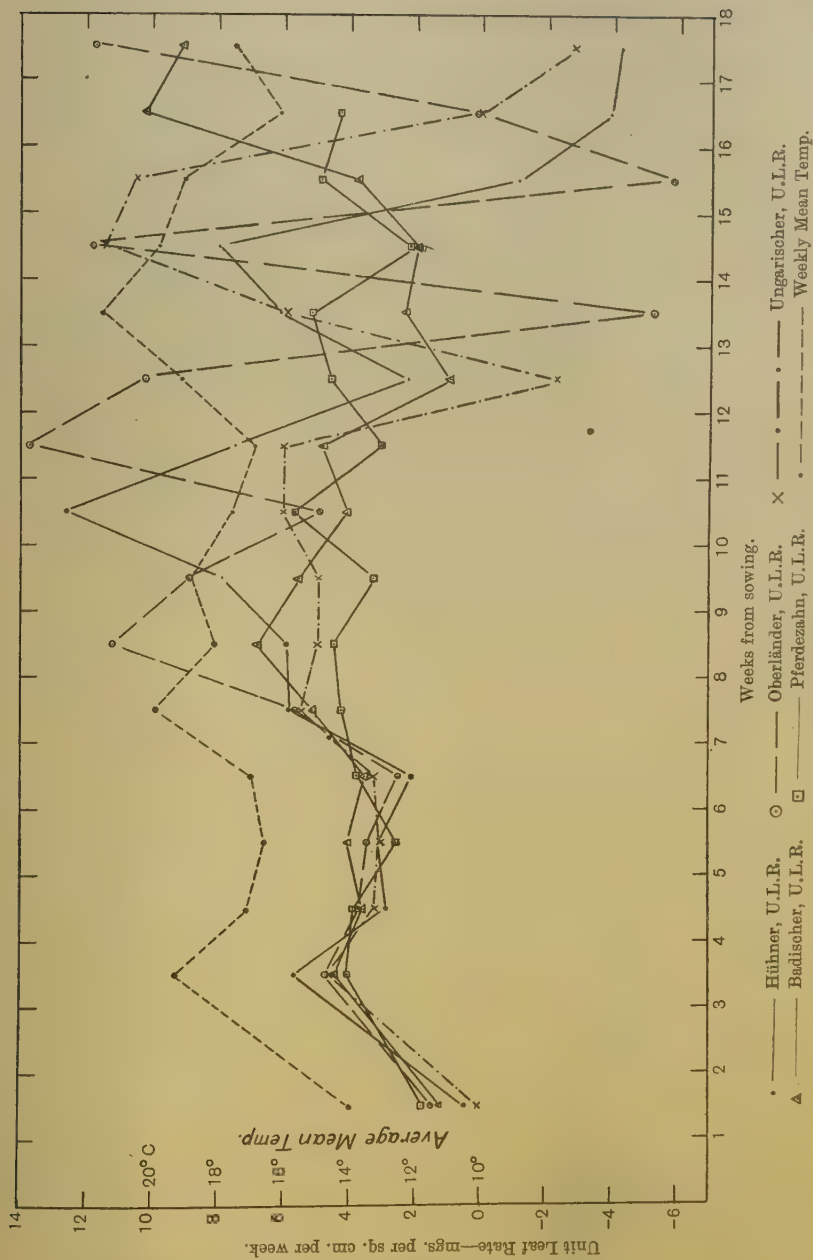


Fig. 3. Five Varieties of Maize — 1875.

values for increase in dry-weight per unit leaf-area vary more or less about a mean and that the fluctuations attain increasing amplitude as the age of the plant increases. We are led therefore now to attempt to correlate these fluctuations with changes in environmental conditions.

Table I.—*Unit Leaf Rate for five varieties of maize grown at Poppelsdorf in the year 1875.*

Week ending	"Hühner"	"Oberländer"	"Ungarischer"	"Badischer"	"Pferdezahn"	Average mean temperature
1st June	0.5	1.2	.05	1.25	1.8	14° C.
8th "	5.7	4.75	4.65	4.45	4.1	19.3
15th "	2.9	3.75	3.25	3.65	3.9	17.1
23rd "	3.15	3.5	3.1	4.1	2.6	16.6
30th "	2.15	2.55	3.3	3.6	3.8	17.0
7th July	5.85	5.7	5.5	5.2	4.3	19.9
13th "	5.95	11.2	5.0	6.9	4.55	18.1
21st "	7.9	8.9	5.0	5.6	3.3	18.8
27th "	12.5	4.9	6.05	4.1	5.7	17.6
3rd Aug.	7.5	13.7	6.0	4.9	3.0	16.9
10th "	2.25	10.2	— 2.25	1.0	4.6	19.1
17th "	6.1	— 5.2	5.9	2.35	5.2	21.5
24th "	8.0	11.8	11.4	2.0	2.2	19.8
31st "	— 1.1	— 5.8	10.5	3.8	4.9	19.0
7th Sept.	— 3.9	.15	0.1	10.2	4.3	16.1
15th "	— 4.2	11.7	— 2.8	9.1	—	17.5

Table II.—*Unit Leaf Rate for "Badischer Früh" maize (1876).*

Week ending	Unit leaf-rate	Average mean temperature ° C.	Hours of sunshine
24th May	—	9.8	—
31st "	— 10.6	13.0	42
7th June	+ 1.39	15.1	61
14th "	2.4	16.3	16
21st "	3.05	16.9	57
28th "	6.83	19.0	102
5th July	5.36	17.6	42
12th "	3.95	20.0	45
19th "	7.54	17.6	71
26th "	6.87	18.5	49
2nd Aug.	8.5	20.3	93
9th "	4.15	18.3	76
16th "	12.5	21.9	94
23rd "	— 0.46	21.6	77
30th "	— 0.43	14.5	10

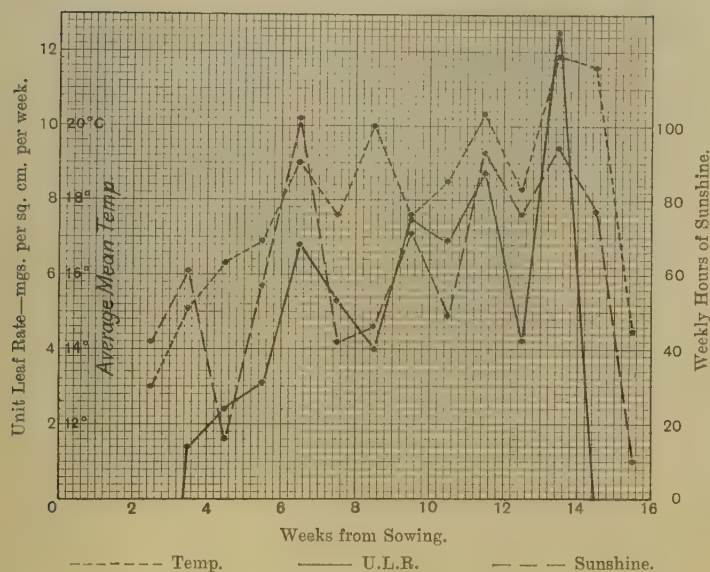


Fig. 4. Badischer Früh-Mais — 1876.

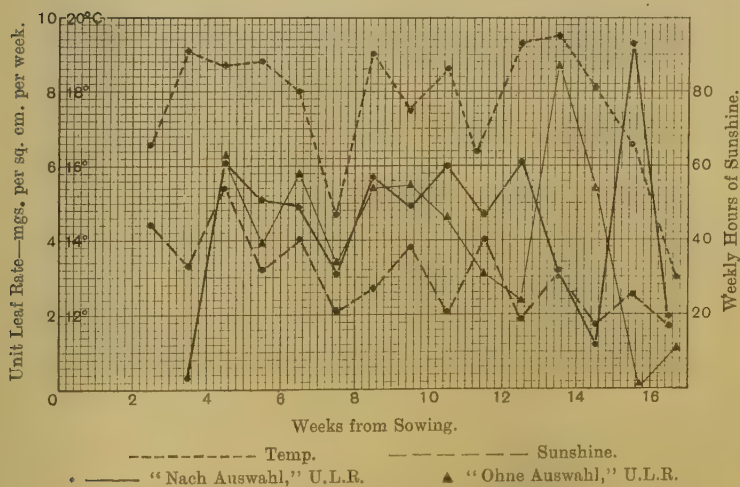


Fig. 5. Badischer Früh-Mais — 1877.

Table III.—Unit Leaf Rate for “Badischer Früh” maize (1877).

	Unit leaf-rate (Nach Auswahl)	Unit leaf-rate (Ohne Auswahl)	Average mean temperature ° C.	Hours of sunshine
29th May	—	—	11.9	14
5th June	-15.0	-15.0	16.6	44
12th „	+ 0.23	+ 0.04	19.1	33
19th „	6.1	6.2	18.7	54
26th „	5.1	3.9	18.8	32
3rd July	4.9	5.8	18.0	40
10th „	3.1	3.4	14.7	20
17th „	5.7	5.5	19.0	27
24th „	4.9	5.5	17.5	38
31st „	6.0	4.6	18.6	20
7th Aug.	4.7	3.1	16.4	40
14th „	6.1	2.4	19.3	19
21st „	3.1	8.7	19.5	30
28th „	1.2	5.4	18.1	17
4th Sept.	9.2	- 0.1	16.6	25
11th „	1.9	1.1	13.0	17

Table IV.—Unit Leaf Rate for “Badischer Früh” maize (1878).

Week ending	Unit leaf- rate	Average mean temperature ° C.	Hours of sunshine
28th May	—	12.4	—
4th June	—	13.6	40
11th „	-3.55	15.5	27
18th „	+2.25	15.1	19
25th „	4.3	17.9	40
2nd July	6.2	19.8	36
9th „	3.9	17.1	16
16th „	4.3	16.8	20
23rd „	6.4	19.6	57
30th „	6.3	19.8	23
6th Aug.	7.6	18.2	35
13th „	3.9	20.1	32
20th „	5.0	19.3	35
27th „	8.8	17.8	17
3rd Sept.	4.6	19.0	21
10th „	-1.1	19.2	35

II. CORRELATION OF UNIT LEAF RATE WITH ENVIRONMENTAL FACTORS.

(1) Sampling errors.

Before attempting to correlate the fluctuations in the values of the Unit Leaf Rate with environmental factors it will be as well to consider to what extent they may be due to sampling errors.

In the case of the results cited above Kreusler states that the seed was selected with care. The weight of the seed seems to have varied, for example, from .35 to .45 gm. in the year 1877. He gives no idea as to the coefficient of variation of the samples of seeds nor does he give the coefficient of variation of the dry-weight of the plants for each harvest, but merely the mean value. One cannot therefore say what is the probable error of the figures given for Unit Leaf Rate. Again, the number of plants taken at each harvest seems to have been determined rather by labour involved than by accuracy of results desired. This is perfectly natural when the magnitude of the work is considered. In the case of

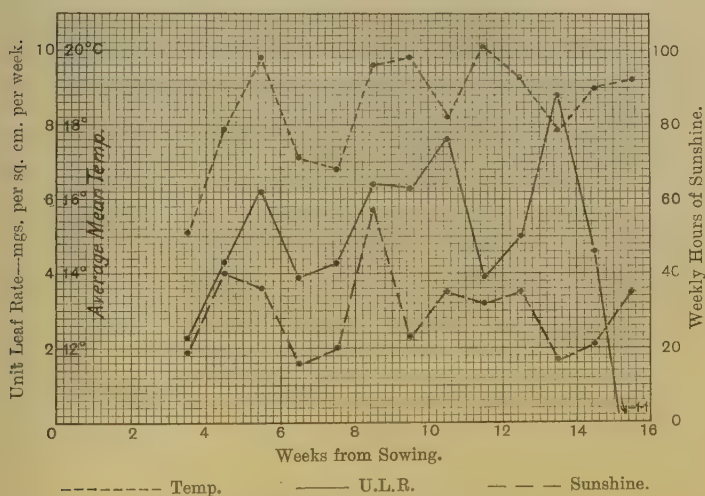


Fig. 6. Badischer Früh-Mais — 1878.

the earlier harvests about 100 plants were used; this number was reduced to about 40 in the later harvests. The number used for the determination of leaf-area was usually one-half the number harvested.

In order to obtain an idea of the order of probable error to be expected, 40 plants were gathered this year by the authors from an ordinary crop of maize. These gave a mean dry-weight of 6.38 gms. with a probable error of $\pm .25$.

In Fig. 3 the Unit Leaf Rate curves for five different varieties of maize grown at the same time under similar conditions are presented. The fluctuations in these curves for the first eight weeks show a good agree-

ment; this may be taken as evidence that the probable error of the mean values up to this stage was sufficiently small not to deprive the fluctuations of significance. The curves A and B, Fig. 5, which are respectively curves for plants selected as mean and for unselected plants of the same variety grown in the same year, add further evidence of the same nature that the results for about eight weeks at the beginning of the life-cycle are comparatively reliable. After the first eight weeks there is no agreement in the fluctuations in the case of the five varieties or in the case of the selected and unselected plants. This lack of agreement may be due in the case of the five different varieties to inherent differences in the plants, and in the case of the selected and unselected to earlier maturity of the unselected. The selected plants were harvested "nach Parzellen," and hence the plants grew in close proximity throughout, whilst the selected ("nach Auswahl") were thinned out at each succeeding harvest.

The following considerations, however, incline us to the opinion that the lack of agreement in the later stages is due partly to sampling error. In the first place, the leaf-area ratio is constantly falling from about the seventh week onwards. For the same coefficient of variation from week to week of the dry-weight of the plants harvested, the probable error of the Unit Leaf Rate will increase as the Leaf Area Ratio falls, provided the Unit Leaf Rate remains roughly constant throughout. We should expect therefore from about the seventh week onwards increasing amplitude of the fluctuations for a given variety, and less agreement in the results from different varieties, as is actually recorded. Secondly, Kreuzler's figures¹ show that whenever a decrease in mean dry-weight is recorded a corresponding decrease in leaf-area accompanies it. It is not likely, except at the end of the life-cycle, that either the dry-weight or leaf-area ever decrease to any appreciable extent, still less that they should decrease together. This is an indication that the larger fluctuations in the later part of the life-cycle and the lack of agreement between crops grown in the same year are due to sampling errors.

In attempting to correlate the fluctuations of Unit Leaf Rate with changes in environmental factors we think it advisable, except in the case of the harvests "nach Auswahl," to neglect weeks subsequent to the eighth.

¹ See tables in previous paper.

(2) *Correlation of Unit Leaf Rate with environmental factors during the early part of the life-cycle¹.*

The environmental factors for which data are given by Kreusler in the different years are as follows (Table V).

Table V.

Year	Rainfall	Weekly average temperature			Hours of sunshine	Total light as sun-hours (Besonnungsstunden)
		Maximum	Minimum	Mean		
1875	+	+	+	+	—	—
1876	+	+	+	+	+	—
1877	+	+	+	+	+	+
1878	+	+	+	+	+	+

+ means data for this factor are recorded.

In calculating the coefficients of correlation with mean temperature and hours of sunshine the procedure was as follows. In the year 1875, since the weekly Unit Leaf Rates of the different varieties showed very good agreement, the average for the five was taken as expressing the best value. In each year only the values for the five weeks subsequent to the initial rise were used, as the evidence before us indicates that these are least subject to variations due to sampling error. Thus we have a total of 20 cases from which to ascertain the correlation with mean temperature. Since the hours of sunshine were the only record of light intensity for three of the years, the correlation coefficients for the hours of sunshine for the last three years were worked out giving a total of 15 cases.

The correlation coefficients are as follows:

With weekly mean temperature, $r = .77$.

With weekly mean temperature (years 1876-8), $r = .64$.

With weekly hours of sunshine (years 1876-8), $r = .47$.

The partial correlation coefficients for the years 1876-8 are as follows:

With weekly mean temperature, $r = .53$.

With weekly hours of sunshine, $r = .24$.

Thus it is seen that the value of the Unit Leaf Rate is governed more by the weekly mean temperature than by the hours of sunshine during the week.

¹ Since the above was written a paper by Brenchley (3) has appeared in which the writer has investigated the correlation between the rate of growth of garden peas grown in water-cultures and environmental factors. In this paper, however, the rate of growth is expressed per unit dry-weight and not per unit leaf-area as in the above.

(3) *Correlation of Unit Leaf Rate of plants harvested "nach Auswahl" with environmental factors.*

The most complete record of the environmental factors presented by Kreusler for one year is that for 1877, the year in which the selected mean plants were harvested. For this year Kreusler not only gives the usual records, temperature, rainfall, sunshine, and total light, but in a separate paper⁽¹²⁾ he gives a very detailed record of the variations in light intensity for each day. The duration of light intensity of the following fractions of full sunlight, $\cdot 05$, $\cdot 1$, $\cdot 2$, $\cdot 3$... 1 , is recorded, the duration for each intensity being measured to the nearest five minutes. From these figures we have been able to determine the duration in minutes of all the light above any given intensity for individual days, and hence for individual weeks at the end of which each harvest was taken. These values are presented in Table VI. Kreusler himself determined the "total light-effect" ("Gesamtlichteffect") by multiplying each light intensity by its duration and summing the results as "Besonnungsstunden." If one attempts to correlate the "total light-effect" with dry-weight increase per unit leaf-area, there is the underlying assumption that this increase is proportional at any moment to the light intensity, that is, is limited by the light intensity throughout. Our knowledge of assimilation would lead us to believe that light limits the rate of assimilation in nature by direct action on the photosynthetic

Table VI.—*Weekly records of light intensity for the year 1877.*

Week ending	Duration in mins. of light 1/20 of sunlight and above	Duration in mins. of light 1/10 of sunlight and above	Duration in mins. of light 2/10 of sunlight and above	Duration in mins. of light 3/10 of sunlight and above	Duration in mins. of light 4/10 of sunlight and above	Duration in mins. of light 5/10 of sunlight and above	Unit Leaf Rate	Hours of sunshine	Total light (in hours)
	* Fractions of duration of light of lower intensities								
19th June	5915	5785	5475	5240	5065	4880	6.1	54	67
26th "	6360	6160	5475	5010	4670	4370	5.1	32	54
3rd July	6410	6055	5445	4915	4655	4415	4.9	40	57
10th "	6080	5670	5010	4455	4020	3660	3.1	20	41
17th "	6620	6190	5580	4995	4560	4210	5.7	27	48
24th "	6360	6105	5535	5155	4840	4585	4.9	38	57
31st "	6485	6115	5475	4915	4490	4130	6.0	20	46
7th Aug.	5965	5550	4970	4650	4400	4225	4.7	40	56
14th "	5550	5370	4955	4450	4060	3725	6.1	19	41
21st "	5730	5430	5050	4715	4405	4100	3.1	30	49
28th "	5625	5125	4530	4045	3670	3325	1.2	17	35

* For example, in the case of light of $3/10$ full sunlight, $2/3$ duration of light of $2/10$, $1/3$ duration of light of $1/10$, and $1/6$ duration of light of $1/20$ sunlight are added.

process only when the intensity is weak, and that normally the factor which limits the assimilatory process is the rate at which the carbon dioxide can reach the chloroplast—the seat of photosynthesis (2). A point to be remembered, however, is that various environmental factors, such as light intensity, temperature, humidity of the atmosphere, etc., may affect the assimilation, not directly by affecting the assimilatory process itself, but indirectly by affecting the degree of stomatal opening and consequently the amount of carbon dioxide which can reach the chloroplast. We have calculated the correlation coefficients between Unit Leaf Rate and the following—

- (1) Duration of light above certain intensities plus the duration of weaker lights diminished by factors as stated below.
- (2) Total light as calculated by Kreuzler.
- (3) Hours of sunshine.
- (4) Duration of light of all intensities.
- (5) Average maximum temperature.
- (6) Rainfall.

Correlation coefficients between Unit Leaf Rate and various environmental factors¹.

$r_{L_1} = .435$	$r_{L_5} = .67$	$r_T = .36$
$r_{L_2} = .60$	$r_{L_6} = .70$	$r_R = -.56$
$r_{L_3} = .77$	$r_L = .54$	$r_{R_1} = .32$
$r_{L_4} = .72$	$r_{L_4} = .38$	

r_{L_1} = correlation coefficient between Unit Leaf Rate and the duration of light, including light down to .05 sunlight;

r_{L_2} = correlation coefficient between Unit Leaf Rate and the duration of light, including light down to .1 sunlight plus half the duration of light of .05 sunlight;

r_{L_3} = correlation coefficient between Unit Leaf Rate and the duration of light, including light down to .2 sunlight plus half the duration of light of .1 sunlight plus a quarter the duration of light of .05 sunlight;

r_{L_4} = correlation coefficient between Unit Leaf Rate and the duration of light, including light down to .3 sunlight plus two-thirds the duration of light of .2 sunlight, a third that of .1 intensity and a sixth that of .05. And so on for r_{L_5} , etc.;

r_L = correlation coefficient between Unit Leaf Rate and total light;

r_{L_6} = correlation coefficient between Unit Leaf Rate and the hours of sunshine;

r_T = correlation coefficient between Unit Leaf Rate and average maximum temperature;

r_R = correlation coefficient between Unit Leaf Rate and rainfall;

r_{R_1} = correlation coefficient between Unit Leaf Rate and rainfall of the previous week.

¹ The fact that the method of calculation used does not give the exact value for the Unit Leaf Rate during the first few weeks, as already pointed out (see footnote, p. 203), does not materially affect the significance of the correlation coefficients. When the Unit Leaf Rates are calculated on the exponential basis the values for r_{L_3} and r_T , for example, become .76 and .34 respectively instead of .77 and .36.

In calculating these correlation coefficients we have omitted the first phase where the young leaves are most probably assimilating at a much lower rate than the normal leaves, and also the phase marked by the high peak at the end of the life-cycle. In calculating r_{L_1} to r_{L_6} the underlying assumption is that light is not limiting until it is lower than the lowest value before deductions are made. For example, in the case of r_{L_3} it is assumed that light is not limiting the Unit Leaf Rate until the intensity is less than .3 sunlight and that at lower values the Unit Leaf Rate is proportional to the light intensity. It will be seen that the best correlation is obtained when we make the assumption that light up to one-fifth full sunlight is limiting.

III. CORRELATION OF REAL ASSIMILATION WITH ENVIRONMENTAL FACTORS¹.

We have investigated the question as to how real assimilation per unit leaf-area is correlated with environmental factors. Unit Leaf Rate is the net result of gain due to real assimilation per unit leaf-area plus salt-uptake less loss due to the respiration of the whole plant per unit leaf-area. As the ratio of ash to total dry-weight is of the order of .06 and undergoes no marked change from week to week (9, 11, 17), the Unit Leaf Rate plus the respiration of the whole plant per unit leaf-area is a fair comparative measure of the real assimilation.

In order to arrive at values for the respiration of maize we determined the respiration of plants about nine weeks old at 2.8°, 10° and 25° C. respectively. The results are given in Table VII.

Table VII.—*Respiration of maize.*

Temperature	Mgs. of CO ₂ per gm. dry-weight per hour.
2.8° C.	0.311
10	0.557
25	1.818

From these results we have calculated the loss in dry-weight per unit leaf-area per week on the basis of the average dry-weight and the average leaf-area, and have thus been able to make an estimate of the real assimilation (Tables VIII and IX)². In making this estimate of loss

¹ Gregory (8) states a few relations between the average rate of assimilation of cucumber plants and the average intensity of radiation, but the figures he gives are too few to establish any general result.

² The respiration is calculated for the average mean temperature for the week. Twenty-four hours per day have been allowed.

Table VIII.—*Calculated average weekly values for real assimilation of "Badischer Früh" maize for the year 1877.*

Week ending	Calculated weekly loss in dry-weight of the whole plant due to respiration gms.	Loss per square centimetre per week due to respiration mgs.	Average mean temperature °C.	Average maximum temperature °C.	Calculated real assimilation per square centimetre per week (including salt-uptake) mgs.
19th June	0.071	9.7	18.7	24.4	6.8
26th "	0.203	0.6	18.8	23.6	5.7
3rd July	0.495	0.7	18.0	23.4	5.6
10th "	0.730	0.5	14.7	18.7	3.6
17th "	2.10	0.9	19.0	23.4	6.6
24th "	3.52	1.0	17.5	23.3	5.9
31st "	6.30	1.5	18.6	22.5	7.5
7th Aug.	7.60	1.6	16.4	21.2	6.3
14th "	12.60	2.5	19.3	23.0	8.6
21st "	16.80	3.1	19.5	24.7	6.2
28th "	15.60	3.5	18.1	22.0	4.7

Table IX.—*Calculated real assimilation for five weeks in early portion of life-cycles.*

Real assimilation mgs. per sq. cm. per week	Average mean temperature	Hours of sunshine	Year
5.2	19.3	—	1875
4.3	17.1	—	"
4.7	16.6	—	"
4.2	17.0	—	"
6.0	19.9	—	"
3.4	16.3	16	1876
3.9	16.9	57	"
7.5	19.0	102	"
5.9	17.6	42	"
4.8	20.0	45	"
6.7	18.7	54	1877
5.6	18.8	32	"
5.5	18.0	40	"
3.6	14.7	20	"
6.6	19.0	27	"
3.2	15.1	19	1878
5.0	17.9	40	"
6.9	19.8	36	"
4.5	17.1	16	"
5.0	16.8	20	"

due to respiration we have not allowed for the probable falling off in the respiration per unit dry-weight with age, but by taking the values

for the respiration of plants of mean age we have done the best we could under the circumstances. The correlation coefficients of real assimilation with various environmental factors are given below.

Correlation coefficients of real assimilation with various environmental factors.

(For years 1875-8.) With weekly mean temperature $r = .78$

(For years 1876-8.) With weekly mean temperature $r = .82$

(For years 1876-8.) With weekly hours of sunshine $r = .60$

(For year 1877, "nach Auswahl.")

$r_{L_1} = -.07$	$r_{L_4} = .29$	$r_L = .17$
$r_{L_2} = +.08$	$r_{L_5} = .28$	$r_{L_s} = .075$
$r_{L_3} = .28$	$r_{L_6} = .26$	$r_T = .56$

The partial correlation coefficients for the years 1876-8 are as follows:

With weekly mean temperature $r = .76$

With weekly hours of sunshine $r = .38$

It will be seen that in the case of the five selected weeks for the earlier portion of the life-cycle for the four years the correlation of real assimilation with weekly mean temperature and with hours of sunshine is of the same order as that between Unit Leaf Rate and these two environmental factors, that for temperature being the greater. In the case of the larger portion of the life-cycle of the selected plants for the year 1877 it will be seen that the correlation with light, no matter how measured, is insignificant, whereas the correlation with maximum temperature is considerably greater than it was in the case of the Unit Leaf Rate.

If the allowances made for respiration approach accuracy the indication is that the real assimilation of the plant is not governed by light¹. Taking into account the whole of the evidence afforded by the correlation coefficients it would seem that the main factor governing real assimilation is temperature. It must be pointed out that the averages of the daily maximum or mean temperatures are not an accurate measure of the average temperature for the days or for the days and nights of the week respectively. The significant correlation of Unit Leaf Rate

¹ If it is found that the apparent assimilation of the leaves is more closely correlated with light than is the real assimilation, then the indications are that light exerts its controlling influence on assimilation under natural conditions, not by acting directly upon the photosynthetic process itself, but indirectly *via* the diffusion stage (stomatal opening, etc.). The data for deciding this fundamental question are not available in the case of maize, but the writers hope to be able to decide this question in the case of *Helianthus* for which they have collected experimental data.

with temperature may mean, either that it is temperature acting upon stomatal opening or that it is growth (*i.e.* utilization of assimilated material) governed by temperature which controls assimilation. More definite evidence is required before an opinion can be given on this point. We are attempting to obtain such evidence in the case of *Helianthus*.

IV. A COMPARISON OF ASSIMILATION VALUES DETERMINED BY THE "GROWTH" METHOD WITH THOSE DETERMINED BY "GASOMETRIC" AND "HALF-LEAF" METHODS.

We have thought it interesting to make a comparison of values of assimilation calculated from results of growth experiments with values obtained by the "half-leaf" method, with leaves attached to or detached from the plant, and by the "gasometric" method with cut leaves.

Unit Leaf Rate, as already stated, is the resultant of the real assimilation, of salt-uptake and of the respiration of the whole plant per cm.^2 per week. The former takes place only during the hours of light; the two latter proceed during the whole twenty-four hours of each day. If the hours of illumination and the values for the respiration of the leaves and of the whole plant and also the value for salt-uptake are known we can calculate a value for the real assimilation or for the apparent assimilation of the leaves.

In arriving at our estimate of the real assimilation for maize we have used Kreusler's data for the year 1877 since this is the only year for which a full record of the light is available. We have utilised the values of the Unit Leaf Rate for the eleven weeks subsequent to the fourth week from sowing, thus omitting the low initial values, which we have good reason to suppose are not the values for normal leaves, and the exceptionally high value at the end. The results from the "nach Auswahl" experiment were used.

The average Unit Leaf Rate for this period is 4.62^1 , and the total hours of light for the eleven weeks number 1118, or a weekly average of 101.7. The total of hours of light after allowance has been made as in column 4, Table VI, is 959, or a weekly average of 87. Using the former value for the light we obtain an average rate for increase in dry-weight per cm.^2 per hour of light of .0456, which is equivalent to 3.65 mgs. CO_2 per 50 cm.^2 per hour. Adopting the other figure for the light we obtain a value of 4.25 mgs. CO_2 per 50 cm.^2 per hour. Making allowance for the

¹ The Unit Leaf Rate calculated on the exponential basis gives a value about 4%, smaller. The real value is intermediate between these two.

loss by respiration and for the uptake of salts, which for this period shows an average of 6.5 per cent., the real assimilation per 50 cm.² per hour is found to be 4.5 mgs. CO₂ per cm.² per hour when making the assumption that all light is equally efficient, and when light below one-fifth total sunlight is limiting the value becomes 5.3.

Müller(18) has shown by the "half-leaf" method that the apparent assimilation¹ of the leaves of monocotyledons as a class is definitely lower than that of dicotyledons. The values obtained for monocotyledons average about 9 mgs. CO₂ per 50 cm.² per hour², the highest being 14 mgs. for *Musa* and the lowest 6.1 gms. for *Cypripedium*. Maize was not used in Müller's experiments. It should be noted that the values given by Müller are average ones determined under varying conditions of illumination, the leaf being left on the plant and translocation being allowed for. It is clear therefore that the value obtained for maize from Kreusler's results, that is, the value obtained for what we propose to call the "growth" method, is distinctly lower than that for monocotyledons as a class determined by the "half-leaf" method. Müller's figures, however, show that in monocotyledons most of the assimilation takes place during the first few hours of illumination and that the rate falls off considerably later. Since his figures are obtained from experiments of only six hours' duration one would expect the value 9 to be much reduced if the experiment had lasted for the whole day.

As Boysen-Jensen(1) came to the conclusion that the values obtained for assimilation by the "gasometric" method give a more accurate value of assimilation under natural conditions than does the "half-leaf" method and since he quotes the results of growth experiments by Weber(21) as confirmatory of this view we think it useful to reconsider this question in the light of other results from growth experiments.

Unfortunately we have no figures for the assimilation of maize determined by the "gasometric" method under natural conditions of CO₂-supply to compare with the results from growth experiments. We can, however, use the results of some growth experiments carried out by ourselves on *Helianthus annuus*. Further, *Helianthus* is a plant which has received a good deal of attention, both "gasometric" and "half-leaf." The results are given in Table X.

It will be seen that the results obtained for assimilation with *Helianthus* by the "gasometric" method are of the same order as the results

¹ Müller's figures do not take into account the respiration of the leaf; this, however would make very little difference.

² The value for CO₂ is calculated as 8/5 of the increase in dry-weight.

Table X.—*Values for assimilation determined by different methods.*

Method "Growth,"	Investigator	Plant	Light	Temperature	Period	Remarks	Value obtained for assimilation mgs. CO ₂ per 50 sq. cm. per hour
"	Kreusler (13, 14, 15, 16)	Maize	Total duration of illumination	Changing	11 weeks	Respiration of plant and salt-uptake al- lowed for	4.5
"	Weber (21)	<i>Helianthus annuus</i>	10 hours per day	"	50 days	"	4.4
"	Present writers	"	Total duration of illumination	"	1 week	Respiration of plant, but not salt-uptake allowed for	8.5
"Gasometric"	Giltay (7)	"	Changing	13°-27° C.	Few hours	At Wageningen, } Apparent assimi- } lation	{ 2.9 (average) { 3.8 (maximum)
"	"	"	"	28°-36° C.	"	At Buitenzorg, Ap- } parent assimila- } tion	{ 3.9 (average) { 7.2 (maximum)
"	Brown and Escombe (6)	"	Diffuse light	20° C. (<i>circa</i>)	"	Apparent assimila- } tion	3.4
"	Boysen-Jensen (1)	<i>Sinapis</i>	Excess light	20° C.	"	Real assimilation	6.0
"	Sachs (19)	<i>Helianthus</i>	Sunlight	25° C.	"	{ Cut leaves, Ap- } parent assimilation	{ 13.0 (maximum)
"	Müller (18)	"	Illumination changing	15.8°-23.4° C.	—	On plant (trans- location allowed for). Apparent assimilation	14.0 (average)
"	"	<i>Allium</i>	"	"	—	"	9.0 (average)
"	Thoday (20)	<i>Helianthus</i>	Sunlight	27°-29° C.	—	{ Cut leaves, Ap- } parent assimilation	{ 9.0 (average) { 13.0 (maximum)

obtained by Weber by the "growth" method, but are distinctly lower than those obtained by the present writers by the same method. Weber's experiments, however, are open to criticism on the ground that his plants were grown in pots, under which condition *Helianthus* does not flourish, and moreover, they were grown in a greenhouse where the light would be considerably less than that under natural conditions. Our value 8.5 is based on experiments carried out under natural conditions. For a certain week, *i.e.*, the fourth from germination, the Unit Leaf Rate was found to be 9.0. During this week the respiration was measured continuously. When allowance is made for the loss in dry-weight due to respiration the value for assimilation becomes 12.3. The real value would probably be slightly higher since the respiration of a plant exposed to the direct rays of the sun would be higher on account of increased temperature—the temperature of our respiration experiments was the shade temperature. The hours of light for this week numbered 116¹. Utilising this figure for the hours of light we obtain a value of 8.5 mgs. CO₂ per 50 cm.² per hour of light. This value 8.5 includes salt-uptake, which at the most would not be more than 7 per cent., thus it is shown definitely, for *Helianthus*, that the values estimated by the "gasometric" method, which moreover does not include the hours of faint light in the earlier part of the morning and in the later part of the evening, do not give a reliable estimate of the assimilation which the plant can carry out under natural conditions. Our figure of 8.5 is smaller than the figure obtained by the "half-leaf" method.

We propose to consider on a later occasion the probable reason for the "growth" method giving lower values than does the "half-leaf" method.

V. SUMMARY.

In this chapter we have continued our analysis of the results of the experiments on the growth of maize carried out by Kreuzler and his co-workers. The rate of growth has been expressed per unit leaf-area instead of per unit dry-weight as in the last chapter. The term "Unit Leaf Rate" is used for the weekly rate of increase of dry-weight in mgs. per sq. cm. The Unit Leaf Rate, instead of undergoing a perfectly definite type of variation, as does the Relative Growth Rate, fluctuates about a mean value. The larger fluctuations which occur in the values for Unit

¹ If it is assumed that light below 1/3 sunlight is limiting, the hours of light become 88 and the value for assimilation 11.2.

Leaf Rate calculated for the later phases of the life-cycle have been attributed mainly to sampling errors.

Correlations between Unit Leaf Rate and various environmental factors have been determined.

The general evidence is that the Unit Leaf Rate is correlated more closely with temperature than with any of the other environmental factors.

By allowing for respiration on the basis of our own experimental results values for the real assimilation were arrived at. These also show a closer correlation with temperature than with light.

The values for assimilation determined from the Unit Leaf Rate are of a lower order than those determined by the "half-leaf" method, but much higher than those determined by the "gasometric" method.

Finally, the authors wish to express their indebtedness to Dr F. F. Blackman for his stimulating criticism and help in this and in the previous chapter.

(*To be continued.*)

APPENDIX.

The definitions and inter-relation of the terms used by the present writers in their analysis of plant growth are as follows⁽²²⁾:

The *relative growth-rate*, R , is the weekly percentage rate at which the dry-weight increases. It may be assumed for purposes of calculation that the increase from week to week takes place exponentially, $\frac{R}{100}$ being the exponent, or that it takes place linearly. Both are approximations. If W be the dry-weight $\frac{dW}{dt} = \frac{RW}{100}$. This formula expresses the relation between R and W assuming the increase takes place exponentially and when integrated the equation becomes $\log_e W_2 - \log_e W_1 = \frac{R}{100}$, where W_2 is the dry-weight at the end of the week, W_1 at the beginning of the week and e the base of the natural logarithms. If it is assumed that the increase is linear $\frac{R}{100} = \frac{W_2 - W_1}{\frac{W_1 + W_2}{2}}$.

Leaf-area ratio, A , is the ratio of leaf-area to dry-weight, that is $\frac{L}{W}$. For simplicity $\frac{L_1 + L_2}{W_1 + W_2}$ is used when making calculations on the

linear basis, L_1 being the leaf-area at the beginning of the week, and L_2 at the end of the week.

Unit leaf-rate, E , is the rate of increase in dry-weight per unit leaf-area per week. Then $\frac{dW}{dt} = EL$ and if the exponential basis be adopted for both leaf-area and dry-weight increase then

$$E = (\log_e L_2 - \log_e L_1) \frac{W_2 - W_1}{L_2 - L_1}.$$

On the linear basis $E = \frac{W_2 - W_1}{\frac{L_1 + L_2}{2}}$, that is, the weekly increase in dry-

weight divided by the average leaf-area.

Relative leaf growth-rate, R_L , is analogous to relative growth-rate and

$$\frac{R_L}{100} = \log_e L_2 - \log_e L_1, \quad \text{or} \quad \frac{L_2 - L_1}{\frac{L_1 + L_2}{2}},$$

according to whether the calculations assume an increase on the exponential or the linear basis.

An inspection of the above definitions and formulae will show that whichever formal conception as to the mode of increase of dry-weight and leaf-area be adopted the Relative Growth Rate is merely the product of the Leaf-area Ratio and the Unit Leaf Rate multiplied by 100. This will be made clear by the following. On the exponential basis

$$R = 100 \frac{\frac{dW}{W}}{\frac{dt}{W}}, \quad A = \frac{L}{W}, \quad \text{and} \quad E = \frac{\frac{dW}{dt}}{L}, \quad \text{hence} \quad R = 100AE.$$

On the linear basis it will be seen that the same relationship holds.

In the present and the previous chapter the linear basis has been adopted as the simpler one, and as being sufficiently accurate for the purposes.

None of the above formulae involves the assumption that R , R_L , A , or E are constant throughout the life-cycle.

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DOUBLE CROSS-GRAIN.

BY J. F. MARTLEY.

(With Plate XIII and 11 text-figures.)

THERE is a certain amount of ambiguity in the meaning of the term cross-grain as applied to wood owing to it being used to describe conditions of grain which are similar in appearance though due to different causes.

The simplest use of the term is in its application to a plank sawn obliquely to the longitudinal axis of a straight grained log. A similar condition of the grain can be seen in planks, especially in the outer ones, which have been sawn from logs of considerable taper.

A more logical use of the term is in the description of planks sawn from a torse or spiral-grained log, for in this case it is impossible to saw a plank without cutting across the grain.

There is still a further type of cross-grain, seen in many timbers native to hot climates, which might be called interlocked or double cross-grain, the investigation of which forms the subject of the present paper.

This grain can often be recognised by a characteristic banded appearance on radial surfaces, due to differences in the reflection of light from a number of zones parallel to the longitudinal axis of the trunk. When such a wood is planed, it is at once evident that the grain in alternate zones is inclined in opposite directions.

This variation in the inclination of the grain can also be demonstrated by making successive tangential splits in a narrow stick sawn transversely off the end of a radial board, when it will be found that the inclination of the grain swings alternately to the left and right of the straight.

In the absence of any specific investigation, the simple spiral grain of torse wood suggested that the grain of these exotic timbers is of the nature of a double spiral, the inclination of the grain alternating with the growth of the tree between a left-handed and a right-handed spiral. It was on this supposition that Professor Groom based the explanation of the warping and twisting phenomena of the dipterocarpous wood called Yang⁽¹⁾.

In order to continue his work on the warping and twisting phenomena shown by these woods and to investigate their structure Professor Percy Groom secured through the kindness of Mr R. S. Pearson, Imperial Forest Economist, India, portions of the trunks, in the form of cylindrical drums several feet or more in length, of the undermentioned Indian trees. These Professor Groom entrusted to me to make this preliminary investigation into the true nature of this type of cross-grain:

<i>Flacourtia Cataphracta</i> Roxb.	Bixaceae.
<i>Pentacme suavis</i> D.C.	Dipterocarpaceae.
<i>Shorea robusta</i> Gaertn.	"
<i>Pterospermum acerifolium</i> Willd.	Sterculiaceae.
<i>Garuga pinnata</i> Roxb.	Burseraceae.
<i>Chloroxylon Swietenia</i> D.C.	Meliaceae.
<i>Cedrela Toona</i> Roxb.	"
<i>Pterocarpus Marsupium</i> Benth.	Leguminosae.
<i>Ougenia dalbergioides</i> Benth.	"
<i>Dalbergia Sissoo</i> Roxb.	"
" <i>latifolia</i> Roxb.	"
" <i>Oliveri</i> Gamble.	"
<i>Xylia dolabriformis</i> Benth.	"
<i>Hardwickia binata</i> Roxb.	"
<i>Anogeissus latifolia</i> Wall.	Combretaceae.
<i>Schrebera swietenoides</i> Roxb.	Oleaceae.
<i>Gmelina arborea</i> Linn.	Verbenaceae.
<i>Mallotus philippinensis</i> Muell.	Euphorbiaceae.
<i>Holoptelea integrifolia</i> Planch.	Ulmaceae.

Before I received the material each drum had been sawn up into a number of half-inch boards of which only two at the most were truly radial. In addition there was a transverse disc, a little over an inch thick, for each species, but there was nothing to indicate whether the disc and drum had been contiguous, or separated, in the log from which they had been sawn.

METHODS OF INVESTIGATION.

The methods of investigation into the course of the grain can be classified under two headings, namely: (1) Preliminary Investigations, and (2) Detailed Investigations. The former deal with the methods of attacking the problem, while the latter are concerned with the actual investigation.

Preliminary Investigations.

As the edges of the boards had not been trimmed off except in *Albizzia procera*, it was an easy matter to assemble the boards and examine the grain on the reconstructed drums.

The species could be separated into two groups according to the grain shown on the surface of the drums but it was impossible to say how far this grouping would hold good for complete trunks.

I. Grain of uniform inclination.

Garuga pinnata came under this heading with a left-handed spiral grain.

Albizzia procera, as far as could be judged, also came under this heading with a straight grain.

Calophyllum sp. (Poon). An examination of a six-foot beam suggested that Poon should be included in this group.

II. Grain of variable inclination.

On the surface of some sectors of a drum the grain might be straight, on others inclined as a right-handed or left-handed spiral and again on others the grain might have a sinuous or serpentine course. The general direction of the grain where it was serpentine was either parallel or inclined to the axis of the trunk. Unlike the other group, there was no transverse level where the grain was uniformly inclined around the circumference.

All the remaining eighteen species came into this group, differing from each other in the degree of inclination shown by the grain and in the length of the undulations where the grain was serpentine. The drums were too short to find the average length of the undulations in the different species. The shortest undulations seen measured between six inches and a foot in length.

Each species had next to be tested for the occurrence of cross-grain which could readily be demonstrated by taking a narrow stick sawn transversely off the end of a radial board and splitting it radially down the centre.

The fracture on the transverse surface under the edge of the splitting instrument will naturally be straight but the fracture on the transverse surface, the reverse to the one struck, will be sinuous, the departures from the straight conforming to the variations in the inclination of the grain since the plane of fracture follows the inclination of the grain.

A radial stick from each species was treated in this manner and direct

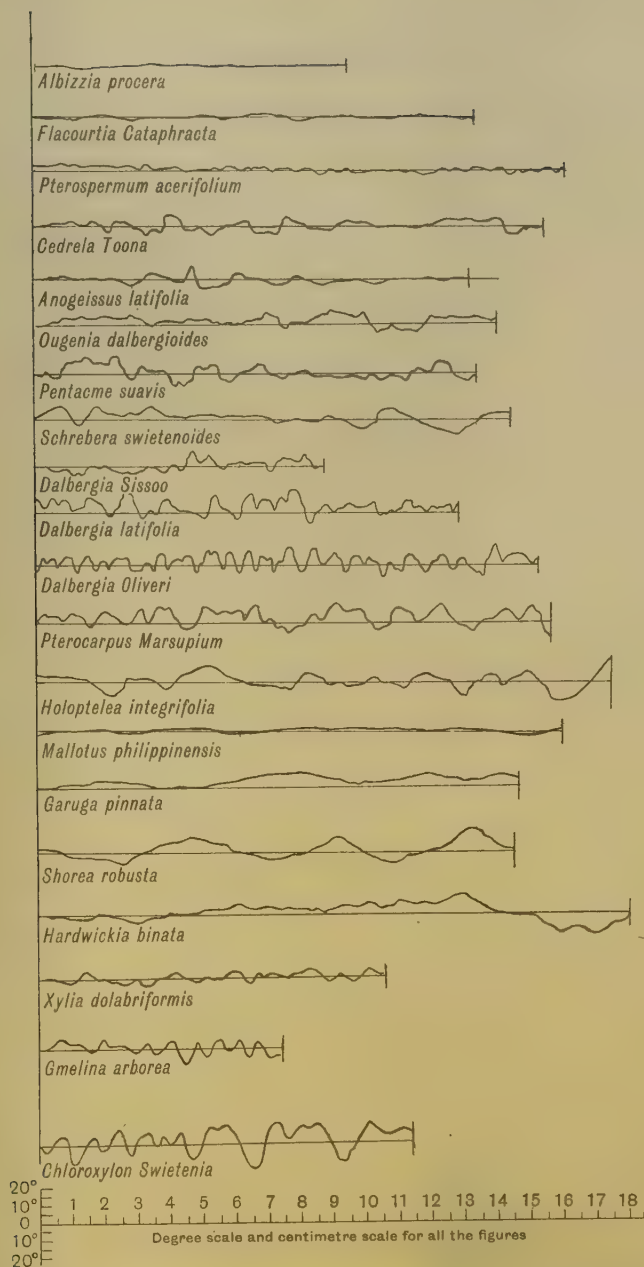


Fig. 1. Outline of a radial fracture for each species obtained from a stick an inch broad, sawn transversely off the end of a radial board.

tracings of the fractures obtained are reproduced in Fig. 1. An examination of the tracings shows that there are all types of gradation from the approximately straight grain of *Albizzia procera* to the uniform type of the double cross-grain characteristic of *Shorea robusta*.

The differences in the character of the cross-grain of the various species appear to be of a quantitative rather than of a qualitative nature, depending on the degree of regularity in the changes in the inclination of the grain, on the average radial distance between the successive right-handed and left-handed phases and on the average angle included between the maximum left-handed and right-handed inclinations of the grain.

The splitting of a radial stick provides a ready means of demonstrating changes of inclination in the grain for a very limited portion of the trunk, but in order to obtain a satisfactory insight into the variations in the inclination of the grain it is essential to know what the appearance of the grain would be like on the surface of the woody cylinder at successive intervals during the life of the tree.

The presence of clearly defined "growth-rings" greatly facilitated this investigation for, on the assumption that they delineated tissues produced at the same time, these rings supplied the necessary time unit without which it would have been impossible to proceed.

In order to obtain a general idea of the course of the grain in a drum use was made of these rings in the case of *Xylia dolabriformis* by splitting successive collars from off the disc at every fifth ring, and by careful planing of a radial board tangentially to the rings. In both cases the inclination of the grain was noted on the successively exposed surfaces.

It was not possible to make detailed records of the variations seen in the inclination of the grain, but the general impression obtained was that there were alternate right-handed and left-handed phases of inclination throughout the drum and that the conformation of the grain on the surface of the woody cylinder was at all times of the type already described under Group II, since, in the radial plane, the grain was often serpentine, its general direction alternating between left-handed and right-handed, and because around any ring in the transverse disc, the grain was never uniformly inclined although its inclination alternated with growth between wholly right-handed and wholly left-handed.

Before proceeding with the detailed method of investigation, a digression is necessary in criticism of the assumption that the rings of these Indian timbers are of the nature of growth-rings.

In dicotyledonous trees, native to temperate climates, the rings are

defined by one or more of the following structural characters (see Groom (2)).

- (1) Variation in the size of the vessels (Oak, Ash).
- (2) Variation in the distribution of the vessels (Apple, Hawthorn).
- (3) Decrease in the radial dimensions of one or more layers of wood elements (Sycamore, Poplar).
- (4) Local decrease in the radial dimensions of the ray cells (Oak, Poplar).
- (5) Local broadening of the rays (Oak, Beech).
- (6) Presence of a more or less continuous sheet of parenchyma (Poplar).
- (7) One or more layers of cells with darker contents.

Where the size and distribution of the vessels is uniform or nearly so and the remaining characters are ill-defined, it is often difficult to recognise a structural limit to the ring under the microscope, although rings can be recognised by the naked eye. This is the case with Boxwood and, to a lesser extent, with Pearwood.

Experience has shown that these rings are annual and are correlated with leaf fall and cessation of active growth before the cold weather sets in, and with the production of fresh foliage when conditions are again suitable for the assumption of growth in spring time.

All the Indian timbers examined in the course of this investigation showed concentric rings which, to the eye, were as well defined as those of many temperate climate trees.

In none of the species examined by the detailed method did the size or distribution of the vessels play any part in the definition of these rings, thus resembling the Willows, Poplars, and Horse Chestnut of this country.

The structural definition of the rings of these species, based on a limited number of sections, was as follows:

In *Chloroxylon Swietenia* the rings were very clearly defined by a layer or sheet of parenchyma two or three cells deep characterised by numerous simple pits.

In *Shorea robusta* the rings were defined by a sheet of parenchyma three or four cells deep. A slight tangential broadening of the rays was apparent where they passed through this sheet. Cysts or canals, probably of schizogenous origin, were of frequent occurrence in this layer.

The ring in *Hardwickia binata* was defined by a layer, three to six cells thick, consisting of parenchyma and of elongated narrow-lumened

cells with brown, resinous looking contents. The walls of the elongated cells were thickly sprinkled with numerous fine pits.

In *Xylia dolabriformis* a layer, one or two cells deep, with darker contents, and apparently fibrous, bounded the rings.

The structural definitions of the rings in *Gmelina arborea* was much less distinct than in the other species although the rings themselves were apparent to the eye. An indistinct layer of parenchyma appeared to delineate the rings.

With regard to the relation between seasonal changes and the periods of growth of these trees, the following information was obtained from Brandis(3):

Chloroxylon Swietenia. Common in the deciduous forests of the Western Peninsula. Flowers March to April. Leaves renewed in May.

Shorea robusta. Never quite leafless. The young foliage appears in March with the flowers.

Hardwickia binata. —

Xylia dolabriformis. Flowers while leafless, in March and April.

Gmelina arborea. Leaves shed from February to April. New foliage appears in May. Flowers from February to April, generally before the leaves are out.

Calophyllum sp. (Poon). Evergreen forests.

Similar seasonal changes are also recorded for the greater number of the remaining species.

The similarity, with regard to the structure of the rings and to the response to seasonal changes, between the Indian trees and the trees of temperate climate indicates that the rings shown in the Indian timbers are of the nature of growth-rings correlated with seasonal changes and lends support to their use as indices of contemporaneity.

Detailed Investigation.

The object of the method adopted was to find the inclination of the grain in every growth-ring of the trunk and to study how the inclination varied from ring to ring.

With the material to hand it was only possible to do this for one transverse and one radial plane of the drum, nevertheless, the data obtained were sufficient for forming a clear idea of the changes which the course of the grain underwent during the growth of the tree.

The rings were counted on the transverse disc of each species ex-

amined, and, to ensure correspondence in numbering along the different radii, the rings were followed completely round the disc. In places where the rings were indistinct, only the more prominent were traced round while the space between two such prominent rings was divided into a convenient number of equal subdivisions.

Where the growth of the tree did not show any great irregularities there would be little error in the contemporaneity of these "pseudo-growth rings" along the different radii of the disc.

After the rings had been counted and numbered, a number of sticks, usually eight in all and at an angle of 45 degrees to each other, were sawn radially out of the discs, care being taken to make the sides of the sticks as near as possible perpendicular to the surface of the disc. The sticks sawn from the disc constituted the transverse series for that species.

The longitudinal series were prepared by sawing a radial board of each species transversely into a number of sticks an inch in depth. The rings were counted on the corresponding transverse surfaces, differences of width and of tint ensuring correspondence in the numbering of the rings in the sticks of each longitudinal series.

Subsequent to the measuring of the width of the rings, the sticks of each transverse and longitudinal series were submitted to the following treatment.

By using a knife each stick was divided up into a number of thin slips by splitting parallel to the rings. So far as the width of the rings permitted a division was obtained between each ring, and in the broader rings as many as three or four splits were easily made. In order to prevent confusion the number of the ring was marked on each slip, a precaution necessitated by the large number of slips obtained from each stick.

The inclination of the grain was then measured on the outer tangential face of the slips and tabulated in conjunction with the width of the rings for each stick.

Lettering the outer face of a slip as in Fig. 2 the grain was traced by means of a lens and a fine needle from the top corner (*B*) or bottom corner (*C*) of the right-hand side *BC*, according to whether the inclination of the grain was right-handed or left-handed, to where it met the opposite side, *CD* or *AB* as the case might be, at the point *X*. By measuring *XC* or *XB* and the side *BC* with a micrometer screw, the angle of inclination of the grain (θ) to the straight could readily be calculated from the tangent.

The inclination of the grain was said to be right-handed and denoted by the sign “/” in the tables when it passed from the top right-hand corner toward the bottom left-hand corner; when it was inclined in the opposite direction it was said to be left-handed and denoted by the sign “\”. When the grain was parallel to the reference side *BC* it was called straight and was represented in the tables by the letter “v.”

The inclination of the grain might equally well have been calculated with the left-hand side, *AD*, of the slips as a basis but for the sake of uniformity measurements were made from the right-hand side only.

The changes in the inclination of the grain along each stick were next plotted diagrammatically in the form of a curve. The rings were plotted along a horizontal line according to their width in centimetres to a scale of 2 to 1. To a scale of 1 mm. to a degree, the inclination of the grain at each ring was plotted in its correct position about the horizontal

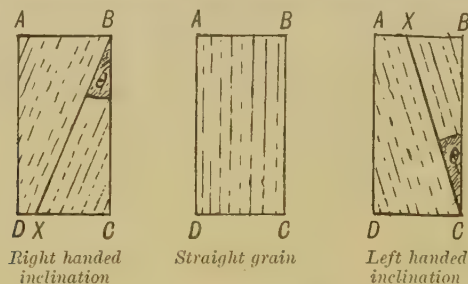


Fig. 2. Method determining the inclination of the grain.

line, degrees of right-handed inclination being plotted above the line, and degrees of left-handed inclination below the line. When the grain was straight the point was plotted in its correct position on the line itself.

On joining these points together a curve was obtained which showed at a glance both the inclination of the grain and the rate of change in the inclination of the grain at any ring.

In order to represent diagrammatically changes in the course of the grain in a radial plane the curves showing the changes in the inclination of the grain along the sticks of the longitudinal series were placed in sequence one above the other. The same procedure was adopted with the curves of the transverse series. On combining the results obtained from the examination of the transverse and longitudinal series of curves a comparatively clear mental picture was obtained in each species

examined of the changes in the course of the grain during the life of the tree.

In order that the individual curves of a series should be more readily comparable among themselves the growth-rings were plotted for all the curves according to their width along a stick of intermediate length. In the longitudinal series this procedure produced no distortion of the curves since in all the species examined the width of the rings remained practically constant through the series, but in the transverse series, on the other hand, a distortion of some of the curves would be caused where the growth of the tree had been excentric. This distortion however will not affect the value of the curves for comparing changes in the inclination of the grain.

In order to test the reliability of the results obtained by this method of investigating the course of the grain, recourse was had to an elaboration of the method of radial fracture already described under the head of "Preliminary Investigations" as the most convenient method for demonstrating double cross-grain.

For checking the longitudinal series of curves, a radial board, if possible adjacent to the one which supplied the material from which the changes in the course of the grain in the longitudinal direction had been derived, was sawn transversely into a number of sticks an inch broad. For ease in subsequent comparison several of the more prominent rings were inked in on the corresponding transverse surfaces of the sticks. Each stick was then split radially, the direction of the split being made in the same sense in each stick. When the sticks were placed in sequence side by side a series of curved fractures was shown which, though not always identical in form, corresponded very closely with the longitudinal series of curves of the same species.

Prior to describing the course of the grain in the different species, it is advisable to mention the errors to which the method of investigation is subject and to estimate their probable effect on the results obtained.

The use made of the rings as an index of contemporaneity has already been discussed. The distinctness with which the individual rings could be followed round the discs and through the longitudinal series reduced errors in the numbering of the rings to a negligible minimum in all except the transverse series of *Gmelina arborea*.

In the actual measurement of the inclination of the grain on the slips repeated tests showed that errors from this source were not likely to have exceeded one degree.

Where the radial board had not been sawn parallel to the axis of

the tree a uniform left-handed or right-handed bias in inclination would be given to the grain as a whole. In no case was there any appreciable inclination between the radial board and the axis of the trunk and in any case provided such inclination was not excessive, the comparative value of the curves would not be influenced since each stick would be equally affected.

The sticks of the transverse series were subject to a similar type of bias which was, however, of a two-fold origin; first to the possibility of the disc not being truly at right angles to the longitudinal axis and secondly to the sides of the sticks not being accurately perpendicular to the transverse surface.

The errors due to the first cause were considered to be negligible, since, as far as could be judged, a disc was never inclined at more than about five degrees to the transverse. The inclination between the sides of the different sticks of a transverse series varied within a range of three degrees at an outside estimation.

As in the longitudinal series errors due to these causes will not affect the comparative value of the curves so far as changes in inclination of the grain are concerned and need only be borne in mind when comparing the inclination of the grain at different points.

As to the sense in which various terms are used the words "Period length," "Amplitude" and "Phase" are employed with meanings analogous to those they possess when used in Physics for the description of wave motion.

The period length is the radial distance between the two maximum inclinations which delimited the period. Amplitude is the angle included between a maximum right-handed and left-handed inclination of the grain. As each period comprises a right-handed or left-handed swing of the grain which are only rarely of equal amount, the average of the two swings is taken as the amplitude of the period. It was on this basis that the ratio of period length to amplitude was worked out.

SHOREA ROBUSTA.

The data regarding the width of the growth-rings and the inclination of the grain at the various rings, from which the two series of curves (Figs. 3 and 4) were constructed are tabulated for the sticks of the transverse and longitudinal series in Tables I and II respectively.

Although in both series the rings were counted from the centre, the numbering of the rings in the two series does not correspond, there being fewer rings in the longitudinal series. This discrepancy is due to two

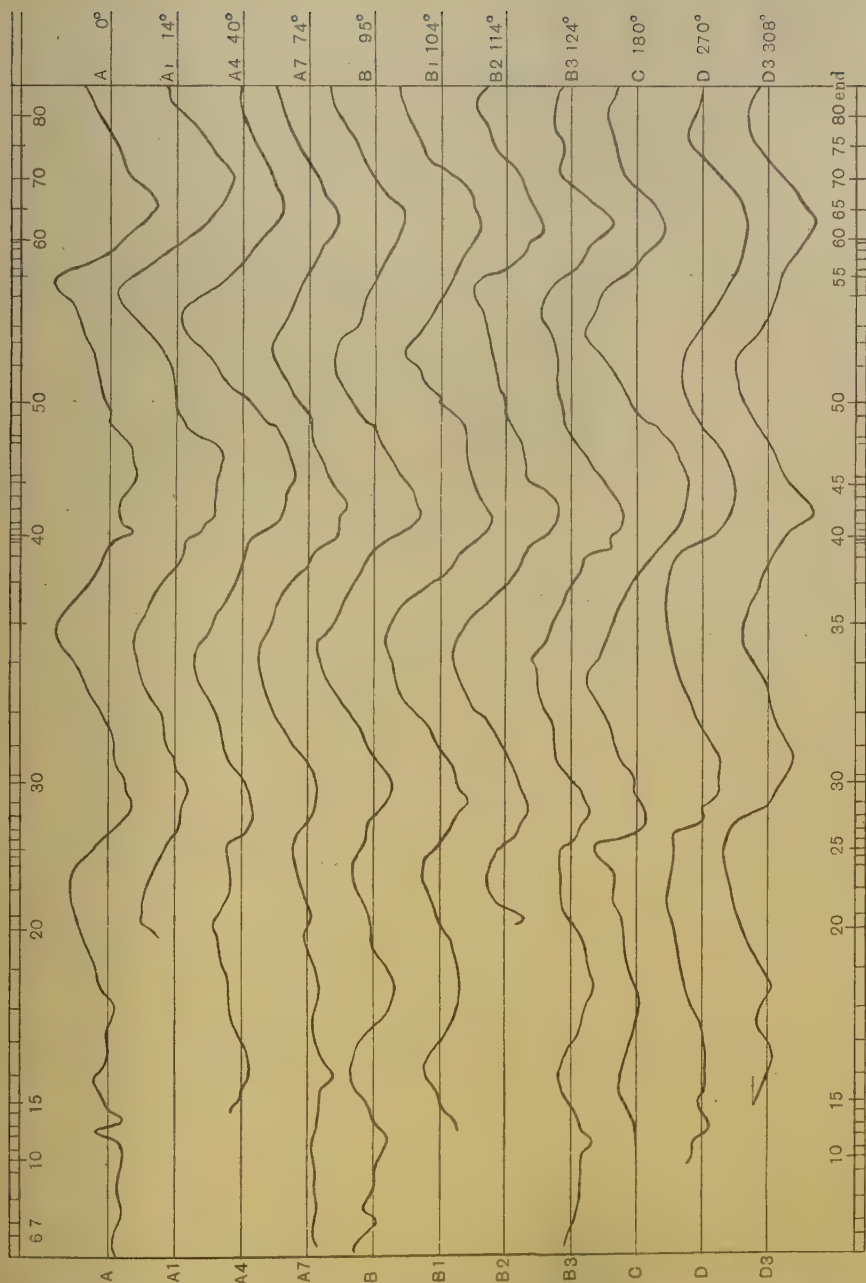


Fig. 3. *Shorea robusta*. Transverse series. The individual curves show the inclination of the grain at the successive rings along the different sticks. The number against each curve gives the angle between that stick and stick A. In each curve degrees right-handed inclination plotted above the base line and degrees left-handed inclination below. Scale: rings plotted to a scale of 2 cm to 1, and inclination of the grain 1 mm. to 1 degree.

Table I. *Shorea robusta*. Transverse series.

The first column of each stick gives distance of each ring in centimetres from the centre, and the second column inclinations of the grain in degrees in the different rings. Where the rings were broad three readings could be taken at the beginning, middle and end of the ring. Straight grain denoted by "v," right-handed inclination by "v," and left-handed inclination by "v."

No. of ring	A	A 1	A 4	A 7	B	B 1
Centre	0 cms.	0 cms.	0 cms.	0 cms.	0 cms.	0 cms.
1	—	0
2	—
3	v
4	3 \	.	.	3 \	6 /	.
5	1 1/2 \	.	.	2 1/2 \	2.00 6 /	.
6	1.30 2 1/2 \	.	.	2.10 2 \	2.28 1 1/2 /	.
7	1.80 4 \	.	.	2.60 3 \	2.50 3 /	.
8	2.15 3 \	.	.	2.90 2 \	2.85 3 1/2 \	.
9	2.25 4 \	.	.	3.05 2 1/2 \	3.25 3 \	.
10	2.45 4 1/2 \	.	.	3.25 1 1/2 \	3.45 1 1/2 \	.
11	2.60 3 \	.	.	3.50 3 \	3.60 4 \	.
12	2.85 v 4 \	.	.	3.60 3 1/2 \	3.80 3 1/2 \	3.25 5 1/2 \
13	3.30 3 \	.	.	3.70 v	3.95 v	3.45 4 \
14	3.95 .	4.15	.	3.80	4.15 1 1/2 /	3.60
15	4.20 .	4.35	v 2 \	3.90 3 1/2 \	4.30 2 1/2 /	3.75 1 /
16	4.60 .	4.65	2 1/2 /	4.65 7 \	4.70 v	4.10 4 /
17	5.00 .	4.80	2 1/2 /	5.15 .	5.18 .	4 1/2 /
18	5.19 1 1/2 \	5.15	3 /	5.75 .	5.70 .	3 1/2 /
19	5.90 .	5.90	6 /	6.35 v	6.30 v	6 1/2 /
20	6.45 .	6.55 6 1/2 /	7 1/2 /	6.95 v	6.90 1 /	5.70 4 \
21	6.60	6.90 9 1/2 /	5 /	7.60 1 \	7.10 .	6.20 v
22	6.85	7.40 7 /	3 /	7.95 .	7.50 2 1/2 /	6.82 1 1/2 /
23	7.25 8 1/2 /	7.55	8.40	7.98 3 /	7.85 6 /	7.05 5 /
24	7.35 4 /	7.62	8.50	8.02	8.00	7.20 3 /
25	7.60 3 /	7.80	8.60	8.05 4 /	8.10 2 1/2 /	7.26 v
26	7.70 v	7.90	8.70	8.15 3 /	8.25 .	7.30 2 \
27	8.10 4 \	8.30	8.95 2 1/2 /	8.25 v	8.40 .	7.48 4 \
28	8.75 7 \	8.40	9.05 3 1/2 /	8.45 2 \	8.60 .	7.74 4 \
29	9.05 5 1/2 \	9.00 4 1/2 \	9.65 2 1/2 /	8.75 2 1/2 \	8.82 4 \	7.90 6 \
30	9.30 5 \	9.50 3 1/2 \	10.15 v	8.95 2 1/2 \	9.10 .	8.42 6 \
31	9.40 3 \	9.70 1 \	10.25 1 /	9.10 2 1/2 \	9.20 1 \	8.68 5 \
32	9.95 2 \	10.20 2 1/2 /	10.90 5 /	9.65 8 /	9.65 4 /	8.80 3 \
33	10.45 3 1/2 /	10.70 6 /	11.55 8 /	10.25 12 1/2 /	10.15 13 /	9.20 7 /
34	11.10 1 1/2 /	11.45 11 /	12.40 12 /	11.05 14 /	10.90 16 /	13 13 1/2 /
35	11.75 14 /	12.00 .	13.00 8 /	11.70 9 1/2 /	11.50 17 12 1/2 /	10.50 15 /
36	12.25 4 1/2 /	12.70 v	13.65 4 /	11.95 v	12.10 9 /	11.04 10 /
37	12.60 .	13.00	13.95 .	12.26 2 \	12.52 3 /	11.60 .
38	12.64 v	13.08 3 \	13.98 2 \	12.34 .	12.68 3 \	12.10 7 \
39	12.67 .	13.16 .	14.01 .	12.40 9 \	12.71 .	12.32 10 \
40	12.70 .	13.25 8 \	14.05 6 \	12.45 9 1/2 \	12.79 8 \	12.40 14 1/2 \

41	12.90	3 $\frac{1}{2}$ \	13.30	8 $\frac{1}{2}$ \	14.10	•	12.55	•	12.90	•	10 $\frac{1}{2}$ \	•	12.46	•
42	13.00	3 $\frac{1}{2}$ \	13.40	12 \	14.20	•	12.65	•	13.00	•	14 \	•	12.53	•
43	13.15	3 \	13.50	12 \	14.35	•	12.75	•	13.20	•	13 \	•	12.60	•
44	13.40	6 $\frac{1}{2}$ \	13.70	12 $\frac{1}{2}$ \	14.50	•	12.90	•	13.36	•	12 \	•	12.85	14 \
45	13.55	8 \	13.90	12 $\frac{1}{2}$ \	14.55	•	13.00	•	13.60	•	9 \	•	13.15	10 \
46	13.75	7 $\frac{1}{2}$ \	14.00	14 \	14.60	•	13.10	•	13.70	•	5 \	•	13.28	•
47	14.05	6 $\frac{1}{2}$ \	14.20	12 $\frac{1}{2}$ \	14.70	•	13.50	•	14.20	•	2 $\frac{1}{2}$ \	•	13.36	•
48	14.55	•	14.70	3 \	14.90	•	13.60	•	14.30	•	2 \	•	13.82	8 \
49	14.95	•	15.05	•	15.10	•	13.85	•	14.00	•	2 \	•	14.00	3 $\frac{1}{2}$ \
50	15.15	2 \	15.15	•	15.30	v	14.00	4 \	14.80	•	6 \	•	14.43	v
51	15.95	4 $\frac{1}{2}$ \	15.30	3 \	15.60	•	14.55	•	15.35	•	10 $\frac{1}{2}$ \	12 \	15.20	9 \
52	16.25	8 \	16.15	8 $\frac{1}{2}$ \	15.85	•	14.90	•	15.70	•	11 $\frac{1}{2}$ \	11 $\frac{1}{2}$ \	15.48	7 \
53	16.45	10 \	16.55	15 \	16.05	•	15.20	4 \	15.95	•	9 \	•	15.70	2 \
54	16.75	16 $\frac{1}{2}$ \	16.85	17 \	16.40	•	15.80	2 $\frac{1}{2}$ \	16.40	•	3 \	•	15.95	2 \
55	17.05	13 $\frac{1}{2}$ \	17.20	11 $\frac{1}{2}$ \	16.75	•	16.20	v	16.80	•	1 \	•	16.05	4 $\frac{1}{2}$ \
56	17.15	6 \	17.35	7 $\frac{1}{2}$ \	17.05	•	16.35	•	16.80	•	2 $\frac{1}{2}$ \	•	16.18	•
57	17.30	v	17.50	3 $\frac{1}{2}$ \	17.25	•	16.50	•	16.95	•	•	•	16.38	7 \
58	17.40	2 \	17.95	v	17.45	•	16.65	4 \	17.10	•	•	•	16.36	9 \
59	17.60	3 $\frac{1}{2}$ \	18.05	2 \	17.55	•	16.80	•	17.20	•	•	•	16.46	•
60	17.80	6 \	18.20	5 $\frac{1}{2}$ \	17.65	•	16.90	•	17.25	•	6 $\frac{1}{2}$ \	•	16.56	11 $\frac{1}{2}$ \
61	17.86	•	•	•	•	•	•	•	•	•	•	•	•	•
62	17.92	10 \	•	•	•	•	•	•	•	•	•	•	•	•
63	17.98	•	•	•	•	•	•	•	•	•	•	•	•	•
64	18.04	•	•	•	•	•	•	•	•	•	•	•	•	•
65	18.10	14 $\frac{1}{2}$ \	18.50	13 $\frac{1}{2}$ \	18.05	•	17.45	•	17.70	•	8 \	•	17.00	10 \
66	18.15	•	•	•	•	•	•	•	•	•	•	•	•	•
67	18.20	•	•	•	•	•	•	•	•	•	•	•	•	•
68	18.25	11 \	•	•	•	•	•	•	•	•	2 $\frac{1}{2}$ \	•	•	•
69	18.30	•	•	•	•	•	•	•	•	•	•	•	•	•
70	18.35	6 \	•	•	•	•	•	•	•	•	•	•	•	•
71	18.42	•	18.90	17 \	18.60	•	17.95	•	18.15	•	•	•	17.50	3 \
72	18.49	4 $\frac{1}{2}$ \	•	•	•	•	•	•	•	•	•	•	•	•
73	18.56	•	•	•	•	•	•	•	•	•	•	•	•	•
74	18.63	•	•	•	•	•	•	•	•	•	•	•	•	•
75	18.70	2 $\frac{1}{2}$ \	19.40	9 $\frac{1}{2}$ \	19.15	•	18.50	•	18.65	•	6 \	•	17.95	5 $\frac{1}{2}$ \
76	18.79	•	•	•	•	•	•	•	•	•	•	•	•	•
77	18.88	•	•	•	•	•	•	•	•	•	•	•	•	•
78	18.97	v	•	•	•	•	•	•	•	•	•	•	•	•
79	19.04	•	•	•	•	•	•	•	•	•	•	•	•	•
80	19.15	2 \	19.95	2 $\frac{1}{2}$ \	19.70	•	19.20	•	19.10	•	12 \	•	18.40	10 $\frac{1}{2}$ \
End	19.80	•	5 \	2 \	20.70	•	19.70	•	19.55	•	13 $\frac{1}{2}$ \	•	18.80	•
			•	2 $\frac{1}{2}$ \	•	v	•	v	•	•	•	•	•	12 $\frac{1}{2}$ \

Table I (continued).

No. of ring	B 2	B 3	C	C 4	D	D 3
Centre	0 cms.	0 cms.	0 cms.	0 cms.	0 cms.	0 cms.
1
2
3
4	.	1.15	.	2 /	.	.
5	.	1.75	.	4 1/2 /	.	.
6	.	1.95	.	4 /	.	.
7	.	2.15	.	2 /	.	.
8	.	2.40	.	4 /	.	.
9	.	2.55	.	2 /	.	.
10	.	3.00	3 \	6 /	4 /	.
11	.	3.55	7 \	4 /	2 1/2 /	.
12	.	3.68	3 1/2 \	v	2 1/2 /	.
13	.	3.80	2 1/2 \	3 \	2 1/2 \	.
14	.	3.85	v	2 /	1 /	.
15	.	4.08	3 /	1 /	1 /	4 /
16	.	4.20	5 /	v	v	v
17	.	4.60	3 \	v	1 /	2 \
18	.	5.18	v	v	1 /	3 \
19	.	5.80	4 1/2 \	8 /	5 /	1 1/2 \
20	6.50	5 1/2 \	5 \	10 /	7 1/2 /	5 /
21	7.10	2 1/2 \	3 \	13 /	9 /	8 /
22	7.45	6.90	2 1/2 \	4.25	10 1/2 /	10 /
23	7.52	7.28	6 /	4.50	10 /	12 /
24	7.62	7.35	5.66	4.56	5.85	13 /
25	7.70	7.42	5.62	4.62	5.90	9 1/2 /
26	7.77	7.48	5.69	4.68	5.95	.
27	8.20	7.54	5.75	4.75	6.00	7.45
28	8.35	7.96	6.20	5.10	6.20	7.52
29	8.80	8.13	6.30	5.20	6.30	7.60
30	9.08	8.60	6.70	5.60	6.50	7.90
31	9.16	8.90	7.05	5.80	6.65	8.20
32	9.60	9.00	7.15	5.90	6.70	8.30
33	10.00	9.50	7.55	6.20	6.95	8.60
34	10.90	9 /	7.95	6.60	7.30	8.95
35	11.50	16 /	8.60	7.10	7.80	9.50
36	12.15	11 /	9.20	7.45	8.15	9.85
37	12.62	3 1/2 \	9.80	7.75	8.25	10.20
38	12.70	6 \	10.25	7.90	8.30	10.50
39	12.80	5 \	10.30	7.95	8.46	10.66
40	12.85	12 1/2 \	10.35	8.00	8.55	10.75

41	12.95	16 \	13.20	16 \	10.45	14½	8.10	8.65	10.80	14 \
42	13.08	16 \	13.30	16 \	10.55	14½	8.20	8.70	10.85	14 \
43	13.20	16 \	13.45	16 \	10.70	14½	8.25	8.80	10.90	14 \
44	13.45	12½	13.65	12½	10.80	15½	8.40	8.90	11.00	10 \
45	13.70	7	13.90	10	10.85	15½	8.50	9.05	11.10	6 \
46	13.90	6 \	14.05	5½	10.90	10½	8.55	9.25	11.20	3 \
47	14.05	4 \	14.15	1	11.05	10½	8.65	9.30	11.50	3 \
48	14.45	2 \	14.55	2	11.25	10½	8.85	9.70	11.60	3 \
49	14.85	v	14.90	v	11.42	v	9.00	10.00	11.85	6 \
50	15.00	v 2½ / 3 /	15.05	3 / 4 /	11.50	5 /	9.15	10.15	12.00	6 \
51	15.55	6	15.60	4 /	12.05	11 /	9.65	10.65	12.50	9 /
52	15.90	7½ /	15.95	6 /	12.45	15½	9.85	11.00	13.00	2 /
53	16.15	10½ /	16.20	9 /	12.80	12 /	10.20	11.40	13.40	4 \
54	16.38	5½ /	16.43	5	13.00	9½	10.80	11.85	13.85	3 \
55	16.48	2 \	16.58	v	13.30	2½ /	11.15	12.25	14.10	4 \
56	16.55	5	16.68	3 \	13.55	6½	11.35	12.40	14.25	6 \
57	16.65	6½	16.80	5 \	13.70	2 \	11.60	12.50	14.40	8 \
58	16.78	—	16.90	6 \	14.25	6 \	11.80	12.70	14.60	10 \
59	16.84	6½	16.98	—	14.35	6 \	12.00	12.85	14.70	10 \
60	16.90	11 \	17.08	10 \	14.45	8 \	12.15	12.95	14.80	12 \
61	.	.	.	13 \	4½ \
62
63
64
65	17.30	8½	17.43	8½	14.95	6 \	12.90	13.50	15.15	11½ \
66
67
68	.	6 \
69
70	17.68	4 \	17.65	4 \	15.35	4 /	13.55	13.85	15.40	4½ \
71
72	.	v	.	2 \
73
74
75	18.10	4 /	18.00	2½ /	15.80	6½ /	.	14.30	15.60	4 /
76	.	5½ /	.	5 /
77
78
79
80	18.58	9 /	18.38	5 /	16.00	9 /	14.55	14.60	15.85	6 /
End	18.90	.	18.75	.	16.50	6 /	15.15	15.10	16.30	3 /

Table II. *Shorea robusta*. Longitudinal series.

The first column of each stick gives distance of each ring in centimetres from the centre, and the second column inclinations of the grain in degrees in the different rings. Where the rings were broad three readings could be taken, at the beginning, middle and end of the ring. Straight grain denoted by "v," right-handed inclination by " / " and left-handed inclination by " \ "

No. of ring	No. 1		No. 2		No. 3		No. 4		No. 5		No. 6	
	cms.		cms.		cms.		cms.		cms.		cms.	
10	0	6 \	1-60	4½	1-60	3 \	1-40	v	1-30	v	1-20	v
11	.	7½ \	.	.	4½	3 \	2 \	.	3½ \	.	2 \	.
12	.	4 \	.	5 \	3 \	1 \	2½ \	.	v	.	v	.
13	.	2½ \	.	1 \	v	v	2½ \	.	v	.	1 \	.
14	.	1 \	.	v	v	v	1½ \	.	2½ \	.	3 \	.
15	1-75	4½ \	3-00	1 \	v	v	v	2-90	2½ \	2-80	3 \	.
16	.	2½ \	.	v	1 \	1 \	1 \	.	2½ \	.	3 \	.
17	.	3 \	.	1 \	1½ \	1½ \	2 \	.	1 \	.	v	.
18	.	2 \	.	v	4 \	4 \	v	.	v	.	2 \	.
19	.	v	5-50	4 \	5-50	4 \	5-30	.	2½ \	5-20	5½ \	.
20	4-40	4½ \	.	6½ \	.	4 \	3 \	.	v	.	v	.
21	.	7 \	.	v	.	2½ \	3 \	.	2 \	.	3 \	.
22	.	3½ \	.	6½ \	.	6 \	3½ \	.	v	.	4 \	.
23	.	v	.	7½ \	.	6½ \	2½ \	.	4½ \	.	9 \	.
24	.	4 \	7-60	7½ \	7-60	6 \	3 \	7-60	v	7-70	3½ \	.
25	6-45	6 \	.	5½ \	.	2 \	3 \	.	2 \	.	v	.
26	.	8 \	.	1½ \	.	4½ \	7 \	.	4 \	.	3½ \	.
27	.	v	.	7 \	.	7½ \	9½ \	.	8 \	.	6 \	.
28	.	4½ \	.	12 \	.	10 \	14 \	.	12 \	.	13 \	.
29	.	10½ \	.	17½ \	.	15½ \	18 \	.	15 \	.	12½ \	.
30	8-90	17 \	10-10	17½ \	10-10	15½ \	18 \	10-00	15 \	10-00	12½ \	.
31
32
33	.	10½ \	.	12 \	.	13 \	14½ \	.	12 \	.	11 \	.
34	.	3 \	10-80	5½ \	10-80	1½ \	3 \	10-60	8½ \	10-60	7 \	.
35	9-65	3½ \	.	3 \	.	v	v	.	2 \	.	v	.
36	.	4 \	.	1½ \	.	1½ \	v	.	v	.	2½ \	.
37	.	4 \	.	7 \	.	7 \	v	.	1 \	.	3½ \	.
38	.	4½ \	.	12 \	.	9½ \	9 \	.	8 \	.	7 \	.
39	.	10 \	11-90	12½ \	11-90	13 \	12½ \	11-70	10 \	11-70	9 \	.
40	10-70	9½ \	.	12½ \	.	13 \	12½ \	11-70	13 \	11-70	12 \	.

41	.	$5\frac{1}{2}/$.	$5\frac{1}{2}/$.	$6 /$.	$5\frac{1}{2}/$.	$7 /$
42	.	$1\frac{1}{2}\backslash$.	$1 \backslash$.	v	.	$2 \backslash$.	$1 \backslash$
43	.	$5 \backslash$.	$4 \backslash$.	$5 \backslash$.	$5 \backslash$.	$5 \backslash$
44	.	v	.	$2\frac{1}{2}\backslash$.	v	.	$1 \backslash$.	$3 \backslash$
45	12.90	$3 /$	14.20	$6 /$	14.20	$4\frac{1}{2}/$	14.10	v	14.10	v
46	$7\frac{1}{2}/$
47	.	$12 /$.	$10 /$.	.	.	$2 /$.	$6 /$
48
49
50	13.35	$10 /$	14.60	$10\frac{1}{2}/$	14.60	$10 /$	14.50	$6 /$	14.50	$7 /$
51	.	$4\frac{1}{2}/$
52	.	$3\frac{1}{2}/$.	$5\frac{1}{2}/$.	$3 /$.	v	.	$2 \backslash$
53	.	.	.	$2\frac{1}{2}/$.	v	.	$3 \backslash$.	$5\frac{1}{2}\backslash$
54	$1 \backslash$.	$3\frac{1}{2}\backslash$.	$7 \backslash$
55	14.15	$3\frac{1}{2}\backslash$.	$4 \backslash$.	$7\frac{1}{2}\backslash$.	$7 \backslash$.	.
56
57	.	.	.	$7 \backslash$.	$10 \backslash$.	$8\frac{1}{2}\backslash$.	$9 \backslash$
58	.	$8\frac{1}{2}\backslash$
59
60	14.80	$12 \backslash$	16.00	$12 \backslash$	16.00	$12\frac{1}{2}\backslash$	15.90	$13 \backslash$	15.90	$13 \backslash$
65	.	$13 \backslash$	16.70	$13 \backslash$.	$15\frac{1}{2}\backslash$.	$14\frac{1}{2}\backslash$	16.60	$15 \backslash$
End	.	.	14\	$13 \backslash$	16.70	$17\frac{1}{2}\backslash$	16.60	$19 \backslash$	16.60	$18\frac{1}{2}\backslash$

41	.	$5\frac{1}{2}/$	$7 /$	$6\frac{1}{2}/$.	$7\frac{1}{2}/$.	$7 /$.	$6\frac{1}{2}/$
42	.	$2 /$	$2 /$	v	.	v	.	$1 /$.	v
43	.	$4 \backslash$	$4\frac{1}{2} \backslash$	$5 \backslash$.	$3 \backslash$.	$4\frac{1}{2} \backslash$.	$3\frac{1}{2} \backslash$
44	.	$2\frac{1}{2} \backslash$	$7 \backslash$	$10 \backslash$	14.00	$7\frac{1}{2} \backslash$	14.20	$9\frac{1}{2} \backslash$	14.10	$8 \backslash$
45	14.00	v	$1\frac{1}{2} \backslash$	$7 \backslash$.	$10 \backslash$.	$10\frac{1}{2} \backslash$.	$10 \backslash$
46	.	.	.	v	.	$5 \backslash$.	$7\frac{1}{2} \backslash$.	$9 \backslash$
47	.	$3 /$	$2 /$
48
49
50	14.50	$5\frac{1}{2}/$	$5 /$	$3 /$	14.50	v	14.60	$2 \backslash$	14.50	$3\frac{1}{2} \backslash$
51	.	v	v	v	.	$2\frac{1}{2} \backslash$.	$4 \backslash$.	v
52	.	v	v	$1\frac{1}{2} \backslash$.	$4 \backslash$.	$4\frac{1}{2} \backslash$.	$3 \backslash$
53	.	.	$3\frac{1}{2} \backslash$
54	.	.	$7 \backslash$	$7\frac{1}{2} \backslash$.	$8\frac{1}{2} \backslash$.	$8 \backslash$.	$9\frac{1}{2} \backslash$
55	.	$6\frac{1}{2} \backslash$
56	.	.	$10 \backslash$	$12 \backslash$.	$10\frac{1}{2} \backslash$.	$10 \backslash$.	$10\frac{1}{2} \backslash$
57	.	$9 \backslash$
58
59
60	15.90	$12 \backslash$	$12 \backslash$	$14\frac{1}{2} \backslash$	15.80	$13 \backslash$	15.90	$13\frac{1}{2} \backslash$	15.80	$13 \backslash$
65	.	$13\frac{1}{2} \backslash$	$14 \backslash$	$17 \backslash$.	$15 \backslash$.	$16\frac{1}{2} \backslash$.	$15 \backslash$
End	16.50	$17\frac{1}{2} \backslash$	$16 \backslash$	$18\frac{1}{2} \backslash$	16.40	$18\frac{1}{2} \backslash$	16.50	$18\frac{1}{2} \backslash$	16.40	$20 \backslash$

Table II (continued).

No. of ring	No. 13		No. 14		No. 15		No. 16		No. 18	
	cms.		cms.		cms.		cms.		cms.	
10	1-20	v	3 /	3 1/2 /	1-10	2 /	4 /	4 1/2 /	45	4 /
11	.	.	v	v	.	1 /	3 /	1 1/2 /	70	v
12	.	1 \	.	3 1/2 \	.	3 /	3 /	1 1/2 \	2	2 \
13	.	2 1/2 \	.	5 1/2 \	.	3 /	3 1/2 \	2 1/2 \	1-30	4 \
14	.	3 1/2 \	.	3 \	.	2-50	1 1/2 \	2 1/2 \	1-70	1 \
15	2-60	3 \	2-60	3 \	.	.	1 1/2 \	3 /	2-10	v
16	.	1 /	.	3 /	.	.	5 /	4 /	2-60	4 /
17	.	2 1/2 /	.	8 1/2 /	.	.	8 /	7 /	3-10	4 /
18	.	7 1/2 /	.	6 /	.	.	6 1/2 /	6 /	3-70	8 1/2 /
19	.	5 /	4-20	5 1/2 /
20	5-00	.	5-00	.	5-00
21	.	3 1/2 /	.	1 1/2 /	.	1 1/2 /	1 1/2 /	v	4-50	v
22	.	3 1/2 \	.	3 1/2 \	.	4 1/2 \	4 1/2 \	6 \	5-10	6 \
23	.	8 \	.	7 \	.	8 \	7 1/2 \	7 1/2 \	5-75	8 1/2 \
24	.	4 \	.	3 \	.	5 1/2 \	5 1/2 \	4 \	6-25	2 1/2 \
25	7-70	v	7-60	3 \	7-60	v	5 /	3 /	7-00	3 1/2 /
26	.	7 1/2 /	.	7 /	.	5 /	6 /	6 /	7-40	9 /
27	.	6 /	.	7 /	.	6 /	6 /	6 /	8-05	7 /
28	.	2 /	.	3 /	.	1 /	1 /	2 1/2 /	8-70	3 /
29	.	4 1/2 \	.	2 1/2 \	.	4 1/2 \	4 1/2 \	3 \	9-30	2 1/2 \
30	10-10	9 \	10-10	5 \	10-10	7 \	7 \	9 \	9-75	5 1/2 \
31	9-80	.
32	9-90	.
33	.	13 1/2 \	.	10 1/2 \	.	9 1/2 \	9 1/2 \	11 1/2 \	10-00	11 \
34	.	9 \	.	7 \	.	7 1/2 \	7 1/2 \	7 1/2 \	10-10	.
35	10-70	6 1/2 \	10-60	4 \	10-70	6 \	6 \	6 \	10-20	4 1/2 \
36	.	3 \	.	1 1/2 \	.	2 \	2 \	4 1/2 \	10-40	3 1/2 \
37	10-50	v
38	.	2 1/2 /	.	4 /	.	2 1/2 /	2 1/2 /	1 1/2 /	10-60	3 /
39	.	6 /	.	8 /	.	6 /	6 /	6 1/2 /	10-90	4 /
40	11-70	11 /	11-60	12 /	11-70	10 1/2 /	10 1/2 /	10 /	11-20	9 /

41	.	5 /	6 /	.	4 /	.	4 /	11.80	3 /
42	.	1 /	r	.	v	.	v	12.30	v
43	.	4 1 /	3 1 /	.	4 \	.	4 \	13.00	5 \
44	.	7 3 /	12 \	.	7 3 /	.	8 \	13.45	9 \
45	14.10	13 \	12 \	14.10	11 \	14.00	12 1 /	13.70	13 \
46	13.80	.
47	.	9 \	9 \	.	11 1 /	.	12 \	13.90	17 \
48	14.00	.
49	14.10	.
50	14.50	4 \	3 1 /	14.50	7 \	14.50	9 1 /	14.20	13 \
51
52	.	v	v	.	2 \	.	6 \	.	.
53	.	1 \	1 /	.	1 \	.	3 \	.	9 \
54
55	.	8 \	4 \	.	r	.	2 \	14.70	5 \
56
57	6 \	.	4 \	.	1 \
58	.	10 1 /
59
60	15.70	12 1 /	9 1 /	15.70	8 \	15.70	7 1 /	15.10	r
65	.	17 1 /	12 \	.	12 1 /	.	10 1 /	.	.
End	16.30	19 \	17 \	16.30	14 1 /	16.30	13 \	15.75	6 \

causes, first, the numbering of the rings was done without comparison between the two series, and secondly, the fainter rings did not stand out so clearly in the sticks of the longitudinal series, with the result that a certain number of them escaped observation. However, the spacing of the rings and the phase of inclination shown by the grain clearly indicate that the 30th to 60th ring inclusive of the transverse series correspond with those numbered from 24 to 50 in the longitudinal series.

The diagram illustrating the longitudinal series (Fig. 4) shows that the curves which indicate the course of the grain in each stick agree together very closely as to form, a fact foreshadowed by the longitudinal parallel zones to be seen on the surface of a radial board, and demonstrate that in a radial plane the inclination of the grain alternates between left-handed and right-handed with the growth of the tree.

On reading off from Fig. 4 the position of each maximum inclination of the grain with reference to the rings, for the successive sticks of the longitudinal series it is seen that the position of each corresponding maximum inclination may remain the same through the series, for example, the one occurring between the 40th and 41st rings, or else it may vary within a range of two or three rings, or finally, as in the last two periods, the position of a maximum inclination of the grain may pass, on being traced through successive transverse levels, more to the exterior or *vice versa*, according to whether the series is examined from the one end or the other.

Thus in *Shorea robusta* it is apparent that though the periods are structurally continuous, their development at different transverse levels in the same radial plane is not necessarily simultaneous, though it usually is so.

From the curves for sticks 1 to 9 (Fig. 4) it is seen that some of the earlier periods do not retain their identity throughout the series; the period comprised between the 12th and 20th rings in stick 6 fades away in sticks 5 to 1, its place being taken by a fresh period. The board, unfortunately, was not long enough to extend beyond this transitional region to where the new period would be fully established.

In some of the other species this fading away of some periods and the increase in the prominence of others was of much more frequent occurrence, and constituted one of the chief causes of lack of correspondence shown by successive curves of a series whether transverse or longitudinal.

That the appearance of this transitional region is not due to errors in the determination of the inclination of the grain is proved by the

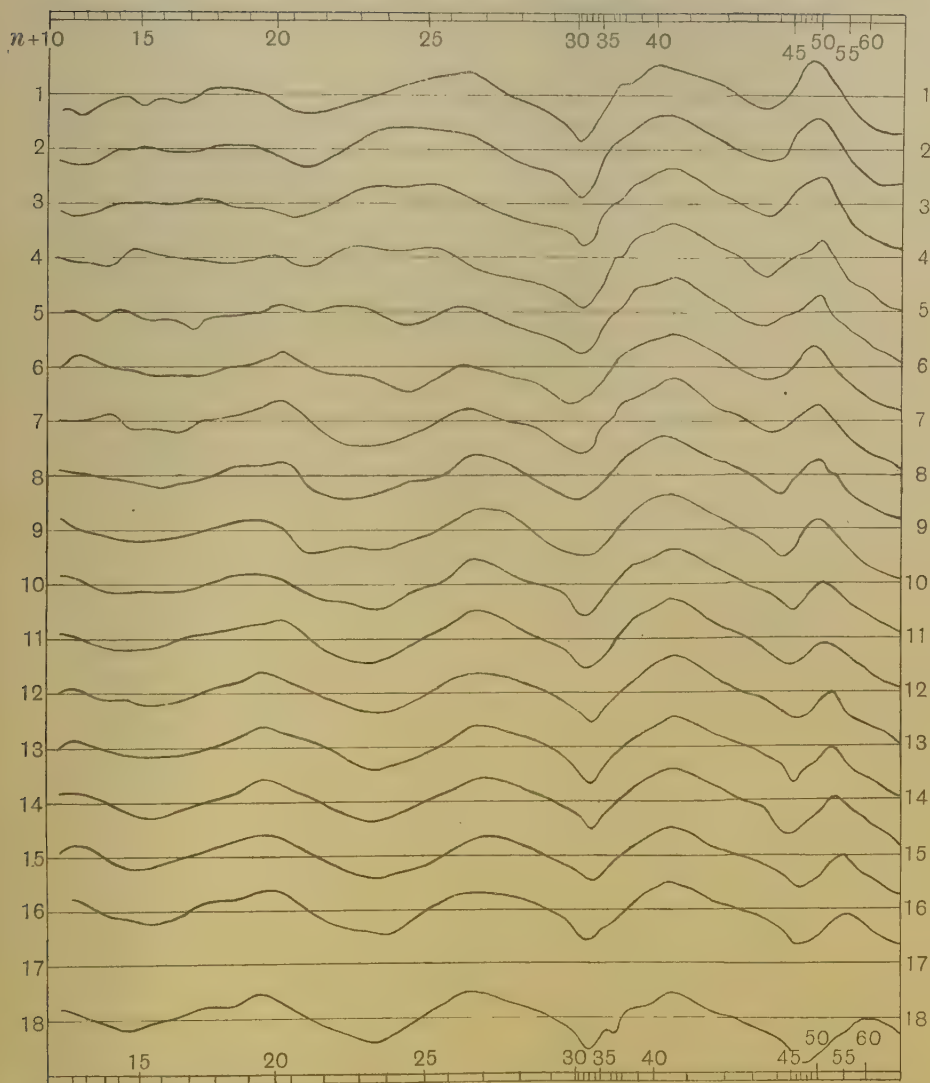


Fig. 4. *Shorea robusta*. Longitudinal series. A series of curves showing inclination of the grain along successive transverse sticks from a radial board an inch apart. Scale as in Fig. 3.

forms of the series of fractures obtained by the radial fracture of a series of sticks sawn transversely from the radial board adjacent to the one which supplied the data for the longitudinal series of curves (photograph 1).

It has already been pointed out that in a radial plane the positions of the periods are not rigidly fixed with reference to the growth-rings, and that there may be a considerable interval between the different transverse levels as to the time of the inception of a period. There is still a further inconstancy discoverable in the series. The actual inclination of the grain at different transverse levels in the same radial plane is not uniform at any ring, but varies in a very undefined manner from stick to stick, and coupled with this is a corresponding variation in the rate of change in the inclination of the grain.

The following example will serve to illustrate these variations. Between the 40th and 41st rings, Fig. 4, there is a maximum right-handed phase in all the sticks of the longitudinal series. Now the inclination of the grain at this point varies in a very irregular manner between 9 and 16 degrees, a range of variation far in excess of the probable error in measurement which was estimated at one degree.

Between the 42nd and 43rd ring the grain has become vertical, hence the rate of change in inclination of the grain could not have been uniform at the different transverse levels.

From the 43rd ring onwards the direction of the change in the inclination of the grain is still the same and reaches a maximum left-handed inclination of five degrees between the 43rd and 44th rings at the level of stick 1, after which the change in inclination of the grain becomes right-handed.

At other transverse levels, however, the grain is becoming still more left-handed, reaching a maximum of 13 degrees at the 45th ring in the 13th stick and of 17 degrees at the 48th ring of the 18th stick.

If the periodic changes in the inclination of the grain were simultaneous with periods of growth and the amplitude of the periods was constant, the grain would consist of a series of alternate left-handed and right-handed spirals (double spiral grain), but on account of the irregularities described above, the grain is composed of a series of superposed serpentine curves grading one into the other which, for short lengths of the trunk at least, tend to be arranged in the form of a double spiral.

The transverse series of curves (Fig. 3) shows a complete parallel correspondence in all points with the longitudinal series. At a transverse level the periodic changes in the inclination of the grain are continuous

tangentially, the periods are not rigidly fixed with reference to the growth-rings, or in other words the periods are only approximately simultaneous, and finally the inclination of the grain at corresponding phases of a period vary from stick to stick. The result is that, though the inclination of the grain alternates between left-handed and right-handed when traced ring by ring from the centre to the exterior, around no ring is the inclination of the grain uniform while often it may change several times from left-handed to right-handed on being followed round. All these points can be followed in a careful scrutiny of the transverse series of curves.

The course of the grain having been determined there still remain some points of secondary importance to be investigated, namely the relations that exist between period length, amplitude, width of rings and age to tree.

In determining average period lengths and average amplitudes all doubtful cases were neglected in transitional regions where one set of periods was vanishing and another set appearing in its place.

The radial distance between two successive maximum right-handed or left-handed inclinations was used for obtaining average period lengths rather than the distance between succeeding vertical phases, since the former was likely to give more reliable figures as it may happen that a period may remain completely right-handed or left-handed in its inclination; for example, the period between the 47th and the last ring in the 16th stick of the longitudinal series which is wholly left-handed.

In Tables III and IV are given the period lengths in centimetres for the sticks of the longitudinal and transverse series respectively, and in addition is given the average period length for each stick and also the average length of the successive periods throughout the series.

The figures in Table III show that the greatest period length (4.15 cms.) in the longitudinal series is reached by the period comprised between the 15th and 23rd rings and that subsequently a decrease in the period length sets in. Correlated with the gradual shift of the last two periods towards the exterior (see Fig. 4) the average period length at the different levels in the longitudinal series shows a gradual increase from stick 6 to stick 18 (last column, Table III).

The measurements of the period lengths of the transverse series (Table IV) demonstrates that the average period length increases with age, as in the longitudinal series, to a maximum (4.35 cms.), after which it decreases. On comparing together the average period lengths of the different sticks it is seen that the period length varies directly with the

radial rate of growth. That this should be so is to be inferred from the excentric growth of the tree and the tangential continuity of the periods in a transverse plane.

Table III.

Shorea robusta. Period lengths in centimetres in the longitudinal series.

Range of period in growth-rings	10-20	15-23	20-26	23-31	26-40	31-45	40-55	Average
	cms.	cms.	cms.	cms.	cms.	cms.	cms.	cms.
6th stick	3.75	4.40	3.40	3.00	3.90	3.65	2.65	3.54
7th "	3.20	3.70	3.45	4.05	3.90	3.50	2.65	3.50
8th "	4.25	3.35	3.70	4.35	3.50	3.80	2.80	3.68
9th "	—	3.85	4.35	4.40	3.50	3.70	2.75	3.76
10th "	3.65	4.20	4.15	3.85	3.75	3.85	2.75	3.79
11th "	4.15	4.35	3.60	4.05	3.65	3.80	2.85	3.79
12th "	3.55	4.25	4.05	4.00	3.60	3.80	2.90	3.74
13th "	3.55	4.10	3.95	4.00	3.65	3.70	2.90	3.70
14th "	3.40	4.10	4.05	4.05	3.60	3.60	3.05	3.70
15th "	3.45	4.30	4.15	4.05	3.40	3.90	3.20	3.78
16th "	3.80	4.35	3.85	3.70	3.50	3.90	3.30	3.77
17th "	—	—	—	—	—	—	—	—
18th "	—	4.50	3.85	2.95	3.70	4.05	3.70	3.96
Average	3.68	4.15	3.88	3.96	3.64	3.77	2.96	3.73
No of rings per period	8	7	7	13	13	13	23	—

Table IV.

Shorea robusta. Period lengths in centimetres in the transverse series.

Range of period in growth-rings	25-35	30-44	35-53	44-63	53-end	Average
	cms.	cms.	cms.	cms.	cms.	cms.
Radial sticks from the disc { A	4.35	4.70	5.50	4.35	3.10	4.40
A 1	4.80	4.60	5.25	4.80	3.70	4.64
A 4	4.10	5.55	3.65	3.40	4.50	4.24
A 7	3.05	3.90	3.85	4.50	5.00	4.06
B	3.35	4.10	4.15	4.50	4.20	4.06
B 1	3.57	4.11	4.58	4.30	3.45	3.99
B 2	3.41	4.40	5.50	3.80	2.30	3.88
B 3	3.50	5.17	5.45	4.00	2.20	4.06
C	2.56	4.55	4.40	3.80	3.35	3.73
D	2.40	2.20	2.45	3.40	3.70	2.83
D 3	2.30	2.45	2.80	4.10	3.35	3.00
Average	3.40	4.15	4.35	4.10	3.55	3.90
No. of rings per period	13	15	18	20	32	—

The magnitude in degrees of the successive right-handed and left-handed swings in the inclination of the grain are given for the longitudinal and transverse series in Tables V and VI respectively. The

Table V. *Shorea robusta*. Table showing the amount in degrees of the successive right- and left-handed swings of the grain for the longitudinal series.

Change in direction of grain and the rings between which included	Left 12th-15th	Right 15th-20th	Left 20th-23rd	Right 23rd-26th	Left 26th-31st	Right 31st-40th	Left 40th-45th	Right 45th-55th	Left 55th-end	Average
1st stick	—	—	9°	15°	26°	28°	16°	17°	27°	—
2nd „	—	—	7	13	25	30	17	15	24	—
3rd „	—	—	6	14	22	29	18	15	27	—
4th „	—	—	5	7	22	31	20	13	27	—
5th „	—	—	—	—	17	28	18	11	26	—
6th „	7°	9°	15	10	14	25	17	12	23	15°
7th „	7	11	16	14	17	28	20	10	25	16
8th „	7	9	13	16	17	23	20	12	22	15
9th „	11	8	12	16	17	22	23	13	22	16
10th „	6	7	13	18	20	24	23	10	20	16
11th „	6	11	15	19	21	25	25	8	16	16
12th „	6	12	15	15	18	25	24	10	22	16
13th „	6	10	16	16	22	25	24	13	20	17
14th „	9	15	16	16	19	22	25	14	19	17
15th „	8	12	16	15	16	20	22	12	17	15
16th „	10	13	16	14	17	21	23	11	—	16
18th „	8	13	18	19	21	20	26	17	—	18
Average swing	8	11	13	15	19	25	20	13	22	16

Table VI. *Shorea robusta*. Table showing the amount in degrees of the successive right- and left-handed swings of the grain for the transverse series.

Change in direction of grain and the rings between which included	Left 25th-30th	Right 30th-35th	Left 35th-44th	Right 44th-53rd	Left 53rd-63rd	Right 63rd-80th	Average	Average period length in cms.
Radial sticks from the disc								
(A	19°	23°	23½°	25°	30½°	23°	24°	4.40
A 1	13	16	26	32	35	22	24	4.64
A 4	14	17½	30	35	31	13	25	4.24
A 7	7	18	27	23	20	20	19	4.06
B	11	23	31	26	21	23	23	4.06
B 1	14	24	33	27	23	25	24	3.99
B 2	12	23	32	26	21	20	22	3.88
B 3	7	18	28	26	23	17	20	4.06
C	16	18	32	32	24	18	23	3.73
D	17	17	21	16	20	18	18	2.83
D 3	21	16	22	24	24	20	21	3.00
Average swing	14	19	28	27	25	20	22	3.90

average (Table V) amplitude remains approximately constant at the successive transverse levels in the longitudinal series, its value ranging between 15 and 18 degrees, but on the other hand the average value of the successive swings increases with age up to a maximum of 25 degrees which is followed by a slight subsequent decrease in value. The figures of Table VI show that the same is true of the transverse series. Although both period length and amplitude reach their maximum value at about the same time, yet the two do not appear to be very closely correlated, for the subsequent decrease in the period length is so much greater than the decrease in the amplitude that the ratio of period length to amplitude steadily decreases with age except for the last period of the transverse series which shows a slight decrease.

On comparing together the average period length and the average amplitude, there are indications that in the transverse series the longer periods are correlated with bigger amplitudes, but no such correlation is apparent in the longitudinal series.

The correlation of period length and amplitude with width of ring is much more indefinite and is only recognisable in so far as all three tend to increase with age up to a maximum which is followed by a greater or smaller subsequent decrease.

CHLOROXYLON SWIETENIA.

The curves of the longitudinal and transverse series are given in Figs. 5 and 6 respectively, but the data from which they have been constructed are not printed here.

The numbering of the rings in the two series is practically identical as the several zones of narrow rings afforded reliable points for comparison.

Due to the uniformity in the rate of growth, the proportional width of the rings remained the same along the different radii of the transverse disc, so the ring widths were only measured along three of the sticks. In the longitudinal series the ring widths were fully measured along one stick from the middle of the series.

An examination of the longitudinal and transverse series of curves shows that the course of the grain in *Chloroxylon Swietenia* is very similar to what it is in *Shorea robusta*. The periodic changes in the inclination of the grain are continuous both longitudinally in a radial plane and tangentially at a transverse level. The inclination of the grain at corresponding points of a period does not remain the same in adjacent sticks of the transverse series or at the different transverse levels in the longitudinal series, a striking instance occurring at the 100th ring of the

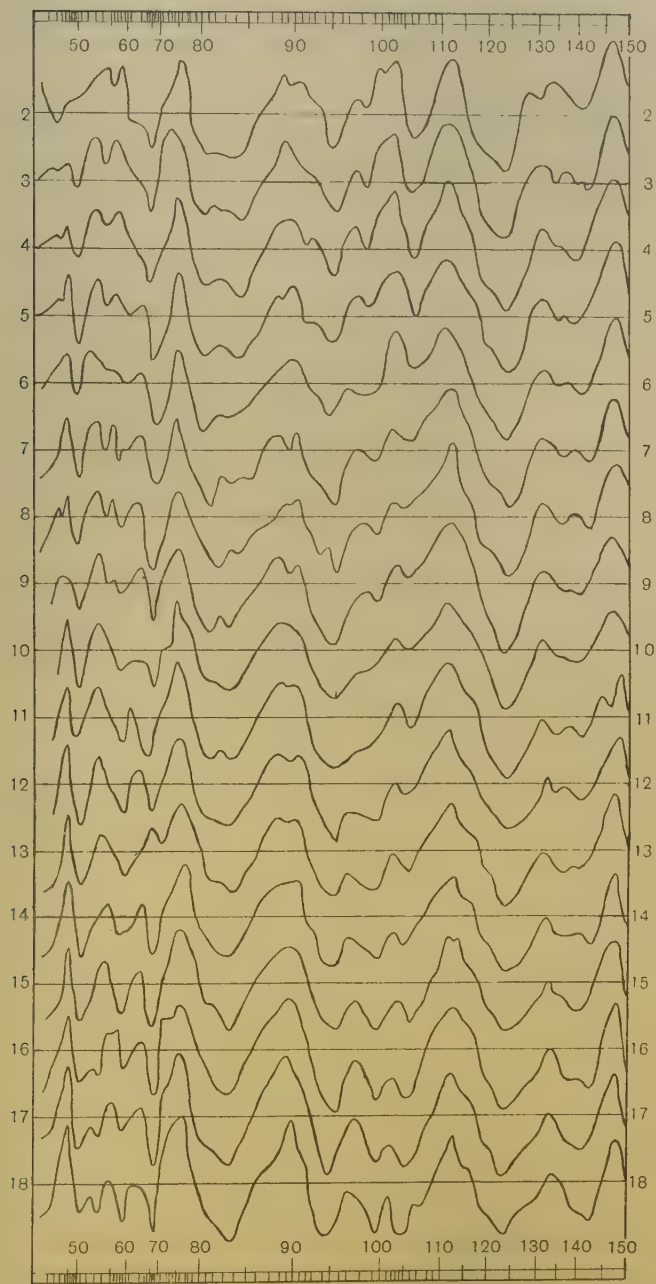


Fig. 5. *Chloroxylon Swietenia*. Longitudinal series. Scale as in Fig. 3.

longitudinal series. The consequence is that the rate of change in the inclination of the grain will not be uniform at any moment, resulting in the grain being composed of a series of superimposed serpentine curves.

Although the general course of the grain in *Chloroxylon Swietenia*

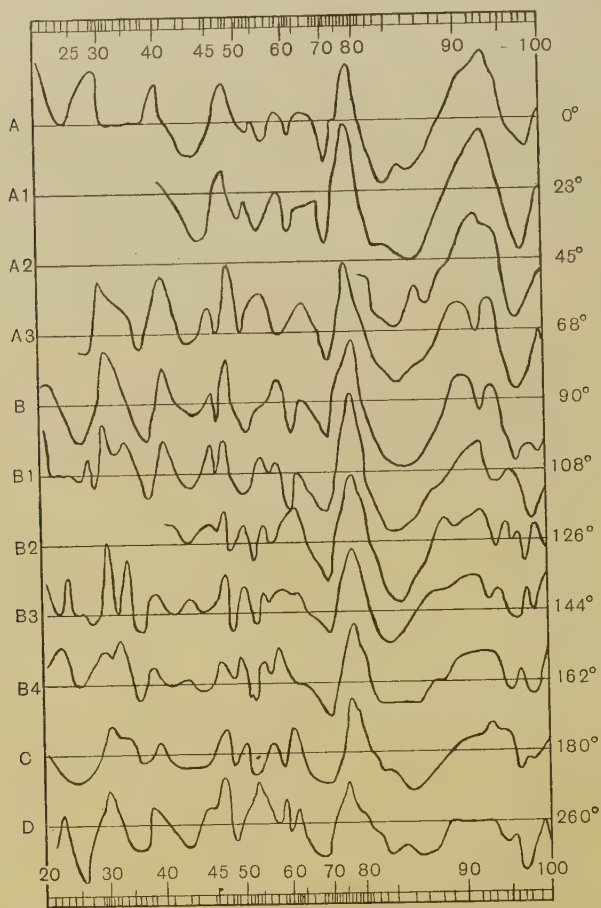


Fig. 6. *Chloroxylon Swietenia*. Transverse series. Scale as in Fig. 3.

and *Shorea robusta* agree very closely together, yet, as might be expected, there are numerous minor differences between the two species.

The length of the period which in *Shorea robusta* ranges between 3 and 4 cms. has an average value of a little less than 1 cm. in *Chloroxylon*

Swietenia. The amplitude is greater in *Chloroxylon*, reaching a maximum of 40 degrees as compared with 30 degrees in *Shorea*.

The net result of a shorter period and a bigger amplitude is that the rate of change in the inclination of the grain will be more rapid, and when this is combined with narrow growth-rings errors in the practical work of investigation will be much more frequent than under the opposite conditions of broad rings and a slow rate of change in the inclination of the grain.

In spite of these disadvantages in *Chloroxylon Swietenia* the Plate, fig. II, of the series of curved fractures obtained by the method of radial splitting, shows that the errors from this source are not so serious as might be expected.

On comparing the position of the periods with reference to the growth-rings in the sticks of the two series it is seen that the periods in *Chloroxylon* are much more closely connected with the growth-rings and show no tendency to cut across periods of growth as in *Shorea robusta*.

Exceptions to this contemporaneity of the periods are due to the somewhat frequent appearance of subsidiary or union periods which retain their identity through a series for short distances only, the period appearing at the 44th ring in sticks A3, B, B1 and B2 if the transverse series is a case in point. Many more of these subsidiary periods can be recognised in the curves of the transverse and longitudinal series.

On account of the frequent appearance of these subsidiary periods it was difficult to obtain data which could be relied on to the relation between period length, amplitude, width of ring and age.

If the 15th stick of the longitudinal series is taken as representing the average condition of the grain for the series it is seen that long periods occur equally where the rings are broad as where they are narrow. No gradual increase in period length, with age, up to a maximum followed by a subsequent decrease is seen as in *Shorea robusta*.

On the other hand it was found on calculating the average that the biggest amplitudes were always correlated with the longest periods.

GMELINA ARBOREA.

The examination of *Gmelina arborea* showed that the grain possesses the same serpentine character that is characteristic of the two species already described.

The method of radial splitting as applied to a portion of the disc showed that the periods are tangentially continuous at a transverse level (see Plate, III). The series of curves which were obtained from the

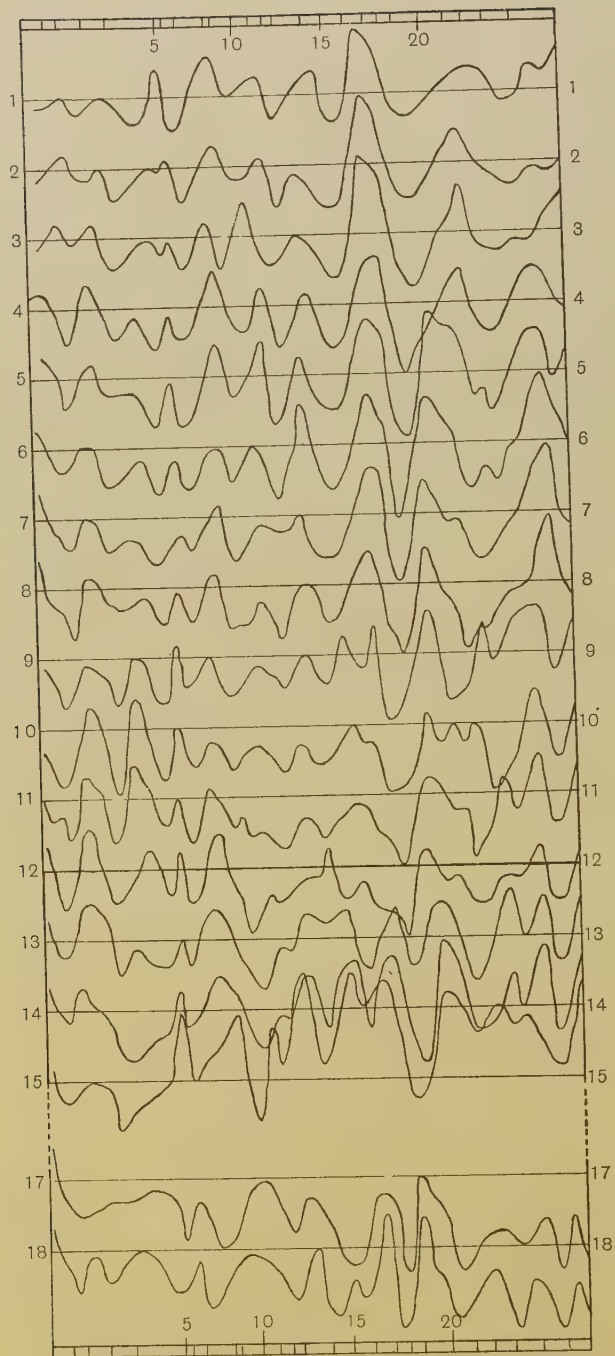


Fig. 7. *Gmelina arborea*. Longitudinal series. Same scale as Fig. 3.

examination of the sticks of the transverse series, however, showed very poor correspondence. This lack in correspondence was due to inaccuracies attributable to the great excentricity of the trunk, the short period

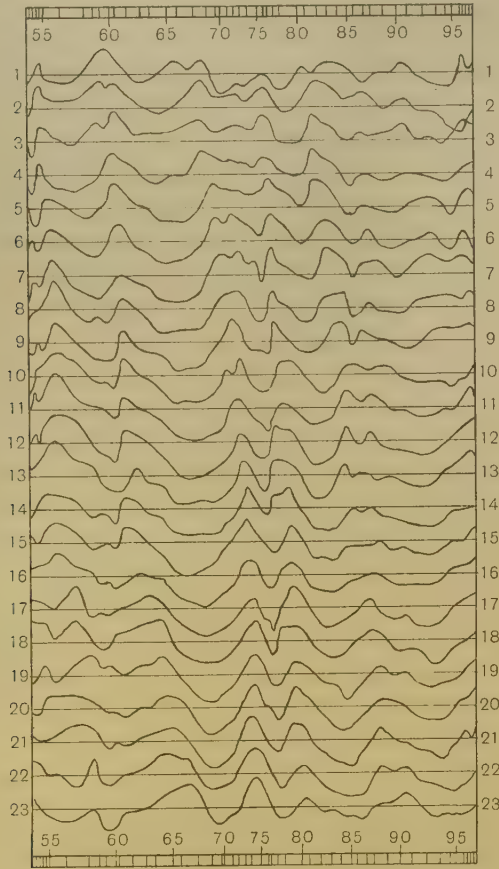


Fig. 8. *Xylia dolabriformis*. Longitudinal series. Same scale as Fig. 3.

length (0.70 cms.) and the frequency with which adjacent rings coalesced for comparatively long tangential distances.

The character of the longitudinal series of curves (Fig. 7) differs in no essential from those of *Shorea* and *Chloroxylon*. The periods are continuous in a longitudinal direction; they are not accurately

simultaneous; and the rate of change in inclination of the grain is not the same at different transverse levels in the same radial plane at the same moment resulting in the prominence of a period varying through the series.

In estimating the average period lengths and amplitudes in the longitudinal series, it was only possible to arrive at approximate values. The figures that were obtained showed that the period length and amplitude had their maximum value near the exterior but no gradual increase in value with age was shown as in *Shorea robusta*.

The disturbance caused by a small branch trace is shown very clearly in sticks 15, 16 and 17 of the longitudinal series. The branch trace passed horizontally outwards at the side of stick 16. The curves of sticks 15 and 17 show that as in straight-grained wood the grain as a whole curves round the knot retaining, however, its cross-grained character.

XYLIA DOLABRIFORMIS.

As the disc had already been used for a general investigation of the course of the grain, it was only possible to examine the course of the grain in detail in the plane of a radial board.

The data for the sticks of the longitudinal series are not printed here but the curves constructed from them are given in Fig. 8.

Taking the results obtained from the investigation of the disc in conjunction with the longitudinal series, it is clear that, as in the other species examined, the inclination of the grain as a whole alternates with growth between right-banded and left-handed, and also, as in the other species, the absence of complete contemporaneity of the periods at the various transverse levels and differences in the rate of change in the inclination of the grain at any moment, result in the grain consisting of a series of superposed serpentine curves.

HARDWICKIA BINATA.

In the transverse series the rings were counted accurately only as far as the 27th ring, after which only the more prominent rings lettered V, W, X and Y were traced round. In each stick the space between each two of these prominent rings was divided up into eight pseudo-growth rings of equal width. This procedure was adopted as the disc had not been smoothed sufficiently for tracing the fainter rings.

In the longitudinal series on the other hand the rings could be counted with precision from the centre to the exterior. As the board did not contain the pith the numbering of the rings in the two series does not

correspond but as far as can be judged the 20th ring of the transverse and the 25th ring or the 26th ring of the longitudinal correspond.

An examination of the longitudinal and transverse series (Figs. 9

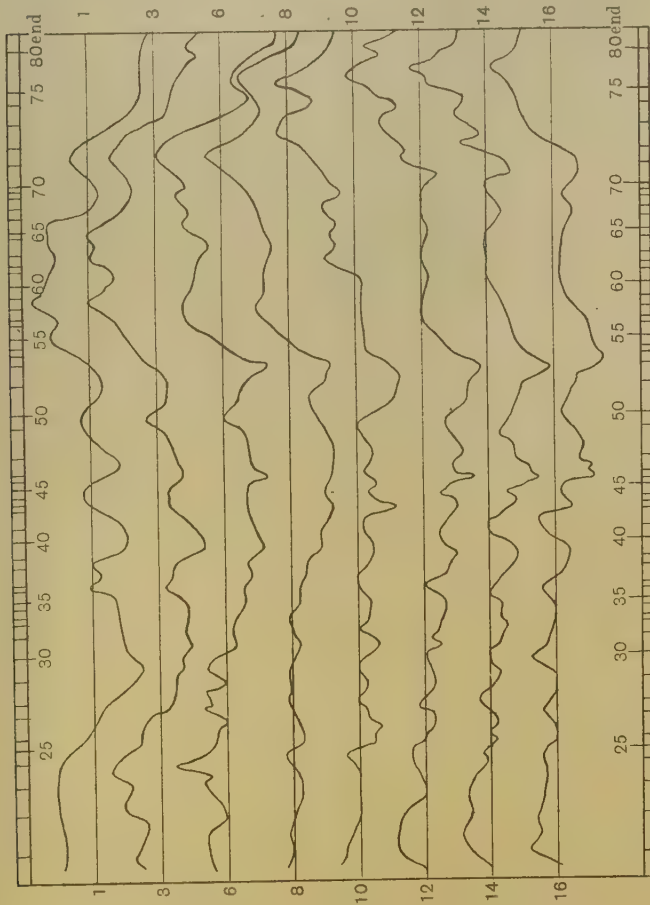


Fig. 9. *Hardwickia binata*. Longitudinal series. Same scale as Fig. 3.

and 10) on the lines adopted for *Shorea robusta* and the other species shows that the serpentine grain of *Hardwickia binata* follows the same general rules as in the species already examined.

In some respects the character of the grain differs from the typical form of serpentine cross-grain as shown in *Shorea robusta* and *Chloroxylon Swietenia*. The longitudinal and parallel zones are not readily distin-

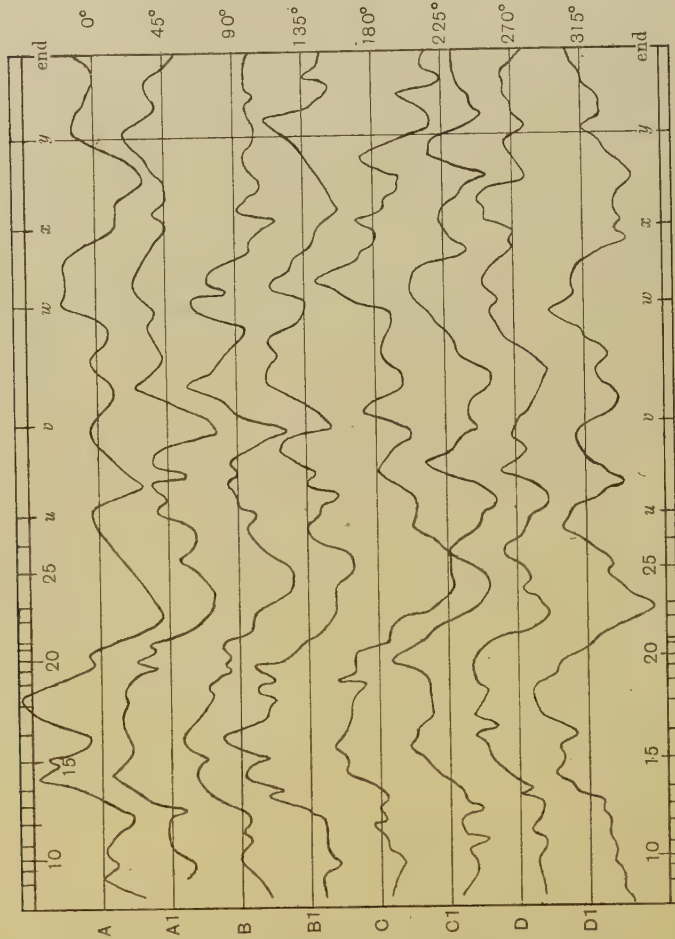


Fig. 10. *Hardwickia binata*. Transverse series. Same scale as Fig. 3.

guishable on a radial board which is due partly to the shortness of the period length and the comparatively small amplitude and partly to periods combining to form compound periods of big extent; stick 3 of the longitudinal series supplying a good example.

Although, as the transverse series shows, these compound periods persist completely round at a transverse level, it seems that they are of only limited longitudinal extent.

*CALOPHYLLUM*¹ SP. POON.

For the material of this species I am indebted to Professor Groom for permission to saw a transverse section off each end of a six-foot beam of Poon wood, 10 inches by 3 inches in section, the longest side of the section being in a radial plane.

The rings were counted on both sections and to ensure identity in numbering every fifth ring was traced from end to end on the radial surface of the beam. The ring nearest the centre was numbered 1 but it was impossible to say how far it might have been from the centre, but the shape of the rings indicated that the beam had been sawn from near the outside of a very large trunk.

The numbering of the rings on the two sections only approximately correspond as difficulty was encountered in tracing the rings along the beam due to the rings frequently fading away, although in many cases they reappeared after a longer or shorter distance.

In Table VII are given the data derived from a radial stick sawn from each transverse section and the corresponding curves are shown in Fig. 11. The rings were plotted natural width and not to a scale of 2 to 1 as for the other species.

The striking feature of Poon wood is the great length of the period ($8\frac{1}{2}$ cms.), being a little more than twice that of *Shorea robusta*. In another specimen of Poon, and probably of the same species, having the same number, four, of rings per centimetre, the period length was 6 cms. This fact suggests that a study of double cross-grain with reference to soil and climate would yield interesting results.

If the rings are used as an index of contemporaneity, though this is somewhat open to doubt for Poon wood, it is seen that the periodic changes in the inclination of the grain are practically simultaneous through a length of six feet, contrasting with the comparatively big shift in the position of some of the periods of the longitudinal series of *Shorea robusta* and *Xylia dolabriformis*.

Judging from the contemporaneity of the periods and the slight variation in their amplitude at the two levels it is to be inferred that the grain in Poon is a true double spiral.

¹ The specific identity of the wood examined was doubtful, though it bore the name of Poon, which belongs to *Calophyllum tomentosum*.

Table VII. *Calophyllum* sp. Spacing of rings in cms. and inclination of grain in degrees along two radial sticks in same radial plane and six feet apart.

No. of ring	Bottom stick		Top stick		No. of ring	Bottom stick		Top stick	
	cms.		cms.			cms.		cms.	
$n+0$	0	$4\frac{1}{2}$ /	0	—	$n+46$	13-15	3 \	13-00	5 /
$n+1$.01	7 /	.20	v	47	13-40	$2\frac{1}{2}$ \	13-30	6 /
$n+2$.35	5 /	.30	$4\frac{1}{2}$ \	48	13-80	$2\frac{1}{2}$ /	13-55	8 /
3	.50	$3\frac{1}{2}$ /	.60	$6\frac{1}{2}$ \	49	14-00	5 /	13-85	$8\frac{1}{2}$ /
4	.70	1 /	.85	v	50	14-20	$7\frac{1}{2}$ /	14-00	$11\frac{1}{2}$ /
5	1-10	2 \	1-10	$\frac{1}{2}$ \	51	14-50	$7\frac{1}{2}$ /	14-20	13 /
6	1-40	$3\frac{1}{2}$ \	1-40	2 \	52	14-75	$6\frac{1}{2}$ /	14-40	$12\frac{1}{2}$ /
7	1-60	5 \	1-65	4 \	53	15-00	$6\frac{1}{2}$ /	14-60	10 /
8	1-80	5 \	1-75	3 \	54	15-25	9 /	14-70	$8\frac{1}{2}$ /
9	2-10	6 \	1-90	6 \	55	15-50	10 /	14-90	8 /
10	2-35	$8\frac{1}{2}$ \	2-20	8 \	56	15-65	$6\frac{1}{2}$ /	15-05	$4\frac{1}{2}$ /
11	2-70	10 \	2-45	9 \	57	15-90	2 /	15-25	4 /
12	3-00	7 \	2-70	$7\frac{1}{2}$ \	58	16-10	1 \	15-50	3 /
13	3-40	9 \	2-95	6 \	59	16-25	$1\frac{1}{2}$ \	15-70	2 /
14	3-70	9 \	3-20	6 \	60	16-50	$2\frac{1}{2}$ \	15-90	3 \
15	4-20	7 \	3-45	5 \	61	16-85	4 \	16-00	$2\frac{1}{2}$ \
16	4-70	4 \	3-90	v	62	17-00	$4\frac{1}{2}$ \	16-20	$4\frac{1}{2}$ \
17	5-10	2 \	4-15	$6\frac{1}{2}$ /	63	17-10	7 \	16-40	$6\frac{1}{2}$ \
18	5-30	v	4-30	$7\frac{1}{2}$ /	64	17-25	$5\frac{1}{2}$ \	16-70	6 \
19	5-60	$1\frac{1}{2}$ /	4-50	$7\frac{1}{2}$ /	65	17-45	$5\frac{1}{2}$ \	16-90	$4\frac{1}{2}$ \
20	5-90	1 /	4-65	$9\frac{1}{2}$ /	66	17-70	$7\frac{1}{2}$ \	17-05	$7\frac{1}{2}$ \
21	6-30	$2\frac{1}{2}$ /	5-00	$11\frac{1}{2}$ /	67	17-90	$8\frac{1}{2}$ \	17-25	9 \
22	6-60	6 /	5-40	$13\frac{1}{2}$ /	68	18-15	$10\frac{1}{2}$ \	17-45	11 \
23	6-90	11 /	5-80	11 /	69	18-40	11 \	17-85	$14\frac{1}{2}$ \
24	7-25	$11\frac{1}{2}$ /	6-30	$8\frac{1}{2}$ /	70	18-50	$9\frac{1}{2}$ \	18-10	11 \
25	7-65	10 /	6-70	5 /	71	18-75	$11\frac{1}{2}$ \	18-30	11 \
26	8-00	9 /	7-20	3 /	72	19-00	$13\frac{1}{2}$ \	18-55	$9\frac{1}{2}$ \
27	8-30	7 /	7-50	v	73	19-25	14 \	18-70	7 \
28	8-60	5 /	7-85	2 \	74	19-50	$15\frac{1}{2}$ \	18-85	5 \
29	8-90	$1\frac{1}{2}$ /	8-15	3 \	75	19-80	15 \	19-05	$3\frac{1}{2}$ \
30	9-15	v	8-45	4 \	76	20-00	11 \	19-25	$1\frac{1}{2}$ \
31	9-45	2 \	8-75	5 \	77	20-20	7 \	19-55	3 /
32	9-65	3 \	9-00	7 \	78	20-40	7 \	19-80	$3\frac{1}{2}$ /
33	9-85	2 \	9-30	9 \	79	20-65	4 \	19-95	3 /
34	10-10	$2\frac{1}{2}$ \	9-60	$7\frac{1}{2}$ \	80	20-85	3 \	20-10	4 /
35	10-35	$6\frac{1}{2}$ \	9-80	13 \	81			20-25	3 /
36	10-70	6 \	10-00	11 \	82			20-40	$4\frac{1}{2}$ /
37	10-90	5 \	10-30	11 \	83			20-70	5 /
38	11-10	$8\frac{1}{2}$ \	10-60	$9\frac{1}{2}$ \	84			20-90	$8\frac{1}{2}$ /
39	11-30	10 \	10-90	8 \	85			21-10	7 /
40	11-55	10 \	11-20	$6\frac{1}{2}$ \	86			21-30	9 /
41	11-70	9 \	11-60	—	87			21-45	$12\frac{1}{2}$ /
42	11-85	$8\frac{1}{2}$ \	11-80	3 \	88			21-65	14 /
43	12-20	$8\frac{1}{2}$ \	12-20	2 \	89			21-85	9 /
44	12-60	6 \	12-50	2 /	$n+90$			22-05	$9\frac{1}{2}$ /
45	12-90	6 \	12-80	4 /					

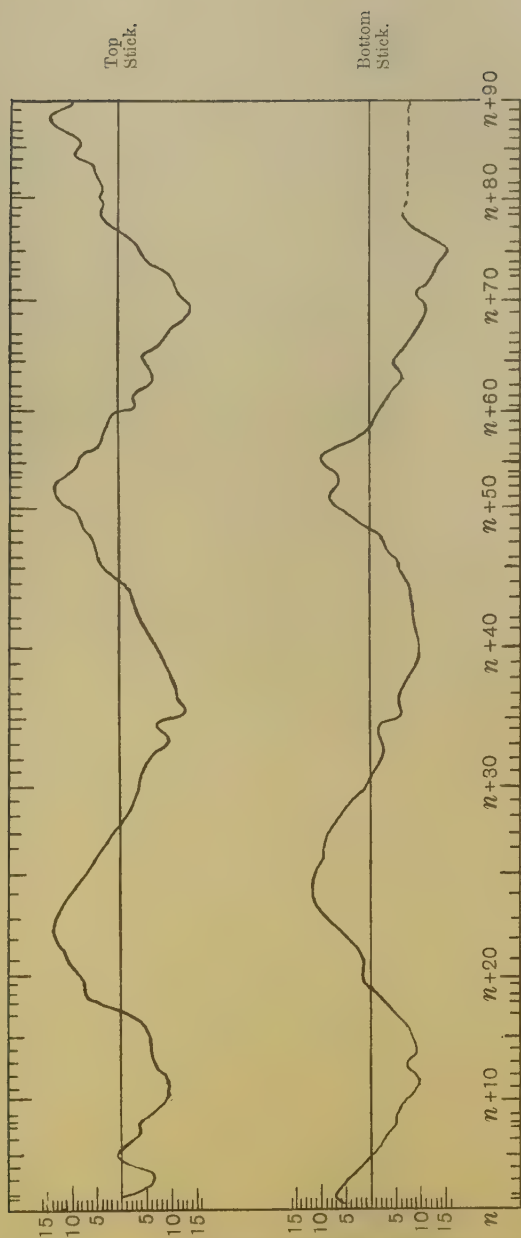


Fig. 11. *Calophyllum* sp. Two curves showing inclination of the grain in two radial sticks six feet apart and in the same radial plane. Rings numbered from "n" to "n+90." Scale: rings plotted natural width and angles of inclination 1 mm. to 1 degree.

Remaining Species.

All the remaining species were examined by the method of radial fracture alone. In no case was any type of cross-grain discovered which did not agree in essentials with that which is characteristic of the species examined in detail.

Even in the straight-grained *Albizzia procera*, slight variations in the grain, too small to be investigated by the detailed method, could be detected which conformed to the same general laws which applied to *Shorea robusta*, etc.

In Fig. IV, of the Plate, are shown the fractures obtained in a portion of the transverse disc of *Holoptelea integrifolia* and, in Fig. V, the fractures in the longitudinal series of sticks.

GENERAL CONSIDERATIONS.

During the course of this investigation several points stood out with sufficient prominence to merit a short discussion anent their probable significance.

The wide distribution of double cross-grain and the uniformity of its character among trees of the most diverse natural orders suggest that it is the expression of some peculiarity common to a large circle of affinity in the vegetable kingdom.

The long series of intermediate forms between straight grain and the full expression of double cross-grain reached by the serpentine cross-grain of *Shorea robusta* and the probable double spiral of *Calophyllum*, and the variation in its development among the members of the same family (see Fig. 1), suggest that there is something, whether of internal or external nature, that inhibits or enhances the expression of double cross-grain, but for the formation of a correct judgment on this point, research is necessary on the influence of local conditions of soil and climate on the development of this type of grain.

There may be, possibly, some correlation between a hot climate and the prevalence of this type of grain, but this can only remain a supposition until temperate climate trees and a larger number of trees from hot climates have been examined from this point of view.

In the attempt to place double cross-grain in proper perspective with reference to other phenomena shown by living objects, a close similarity was found to exist between the changes in the inclination of the grain and the phenomenon of periodicity.

Periodic phenomena among living organisms can be classed under

two heads. Under "Induced Periodicity" are included all those cases which show a more or less direct correlation with the rhythm in external conditions; for instance diurnal and seasonal changes are reflected in the periodicity shown by growth and leaf-fall.

Under "Innate Periodicity" are included all those cases in which no correlation can be demonstrated to exist between the rhythm shown by a living object and the rhythm in external conditions, examples being the alternating streaming movements of the protoplasm of Myxomycetes and the leaf-fall of trees of tropical climates which are characterised by, at the most, only feebly marked seasonal changes (Schimper(4)).

It is under this latter head that the phenomenon of double cross-grain naturally falls for, relying on the evidence of the rings, no correlation could be established between seasonal changes and the period of the grain.

Some interesting analogies are shown between double cross-grain and the leaf-fall of trees native of regions showing absence of seasonal changes (see Schimper). Corresponding with the full development of double cross-grain are those trees which completely shed their foliage at regular intervals varying from two to twelve months, irrespective of the time of year. Trees in which the periodicity of the cross-grain is synchronous only within narrow limits in the trunk are paralleled by those trees which, considered as a whole, are evergreen, but in which the individual twigs are alternately bare and clothed with foliage.

If this type of grain is the expression of some periodicity in the life processes, it is to be expected that other periodic variations, synchronous with the variations in the inclination of the grain should be found. With this object in view the fibre lengths in *Chloroxylon Swietenia* and in *Calophyllum* were determined along a stick at points where the grain was straight and where it was inclined at a maximum.

The figures which are shown in Table VIII are very suggestive, but the inference that there is a correlation between a longer fibre length and inclined grain has no very sound statistical basis for 500 is not a large enough basis for determining a mean where the deviation from the mean is so large in comparison to the difference in the mean fibre length of the successive samples.

Since very little is known of the mechanical effects due to the increase in length of the young fibres it is impossible to say whether the changes in the inclination of the grain might be directly attributable to a variation in fibre length such as is indicated above. The impression obtained, however, during the course of the investigation was that the changes in

the inclination of the grain were due to changes in the orientation of the cambial cells and that the fibres elongated in the direction in which they were laid down when cut off from the cambial cells and that it was not exigencies of spaces that caused their deviation from the straight.

Table VIII. *Chloroxylon Swietenia*. Variation in the mean fibre length with inclination of the grain.

Ring and direction of inclination of grain	76th/	78th v	83rd\	85th v	88th/	92nd v	94th\	97th v	99th/
Basis (number of fibres measured)	502	400	500	496	500	600	288	507	530
Mean fibre length in mms. ...	1.050	1.02	.965	.982	.990	.954	1.040	.968	1.030
Mean deviation from mean fibre length in mms.125	.151	.123	.145	.140	.159	.160	.137	.110
% of fibres within the mean deviation	54	54	53	60	57	58	53	58	57
	108th v	112th/	118th v	124th\	132nd v	140th\	144th v	148th/	150th v
Basis (number of fibres measured)	500	515	424	330	314	468	459	382	481
Mean fibre length in mms.935	.875	.845	.900	.817	.844	.826	.854	.847
Mean deviation from mean fibre length in mms.107	.102	.109	.110	.100	.105	.82	.102	.110
% of fibres within the mean deviation	59	56	56	57	57	57	57	57	56

Table IX. *Calophyllum* sp. Variation in the mean fibre length.

Ring and direction of inclination of grain	(n+3)th \	(n+10)th v	(n+17)th /	(n+25)th v	(n+34)th \	(n+37)th v
Basis (number of fibres measured)	100	100	100	100	100	100
Mean fibre length in mms.	1.160	1.080	1.160	1.020	1.140	1.110
Max. fibre length in mms.	1.710	1.460	1.660	1.450	1.610	1.800
Min. fibre length in mms.	.780	.760	.810	.680	.840	.790

With regard to its commercial aspect the economic value of a study of cross-grain lies in its application in the practice of seasoning wood. The main problems in the seasoning of wood centre round the differences in the rate of loss of moisture and in shrinkage during drying in radial, tangential and longitudinal directions, hence knowledge of the degree of cross-grain shown by different woods is essential if the economic mean between care expended and time involved is to be gauged.

SUMMARY.

1. The character of the double cross-grain of the different Indian woods examined is remarkably uniform and conforms to the following generalisations:

(a) The grain alternates between right-handed and left-handed in inclination during the growth of the tree, these changes in the inclination being in general synchronous in the trunk at least over lengths of two feet.

(b) That the grain does not consist of alternate right- and left-handed spirals is due to the rate of change in inclination of the grain not being uniform at any moment during the growth of the tree either in a tangential or longitudinal direction with the result that the double spiral character is obscured, giving place to a serpentine configuration.

2. Transitional types of grain between straight grain and the full development of double cross-grain are due to variations in the—

(a) regularity shown in the length of the successive periods,

(b) regularity in the amplitude of the successive periods,

(c) stability of the periods over longer or shorter tangential and longitudinal distances.

3. No correlation could be inferred, from the data available, as existing between seasonal changes or periods of growth and the periodicity shown in the inclination of the grain.

There were indications, however, that both period length and amplitude increased with age up to a maximum, and that a long period length was correlated with a big amplitude. Period length responds to the general rate of growth for, in trees of excentric growth, the period length was shortest along the smallest radius.

4. Fibre measurements in *Calophyllum* sp. and *Chloroxylon Swietenia* suggest that a longer fibre length is correlated with inclined grain and a shorter fibre length with straight grain.

5. The character and widespread occurrence of double cross-grain indicate that it is the expression of some periodic phenomenon whether of internal or external nature, but it remains to be seen to what extent a more extended investigation will bring it into line with other periodic phenomena shown by living organisms.

This research was carried out in the Woods and Fibres Department of the Imperial College of Science and Technology, South Kensington, while the author was in receipt of a studentship from the Department of Scientific and Industrial Research.

In conclusion I wish to record my thanks to Professor Percy Groom for suggesting this investigation, providing the material and for help throughout the progress of the work.

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- (1) GROOM, P. Shrinkage, Swelling and Warping of Cross-grained Woods. No. 1, Yang. *Dipterocarpus* sp. *Annals App. Biol.* **III**, 1916.
- (2) — The Evolution of the Annual Ring and Medullary Rays of *Quercus*. *Ann. Bot.* Vol. **XXV**, 1911.
- (3) BRANDIS, D. *Indian Trees*, 1911.
- (4) SCHIMPER, A. F. W. *Plant-Geography*. English edition, 1903.

DESCRIPTION OF PLATE XIII

I. *Shorea robusta*. The series of fractures obtained by radially splitting sticks sawn transversely an inch broad, from an 18 inch radial board. Several of the more prominent rings inked over.

II. *Chloroxylon Swietenia*. Prepared as in I.

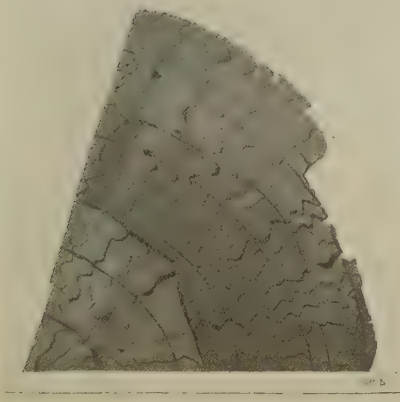
III. *Gmelina arborea*. Radial fractures obtained in a portion of the transverse disc. Several rings inked in.

IV. *Holoptelea integrifolia*. Radial fractures in a portion of the transverse disc.

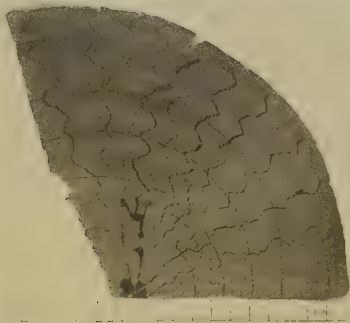
V. *Holoptelea integrifolia*. Longitudinal series of fractures prepared as in I.



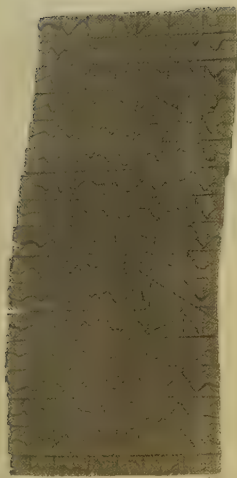
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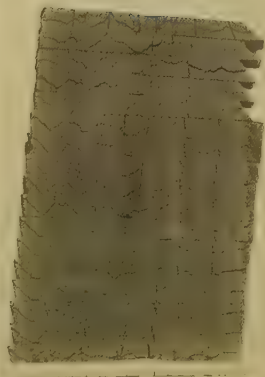
III



IV



II



V

BIONOMICS OF WEEVILS OF THE GENUS SITONES INJURIOUS TO LEGUMINOUS CROPS IN BRITAIN.

BY DOROTHY J. JACKSON, F.E.S.

(With Plates XIV-XIX and 6 Text-figures.)

Read by Dr R. STEWART MACDOUGALL, July 3rd, 1919.

PART I.

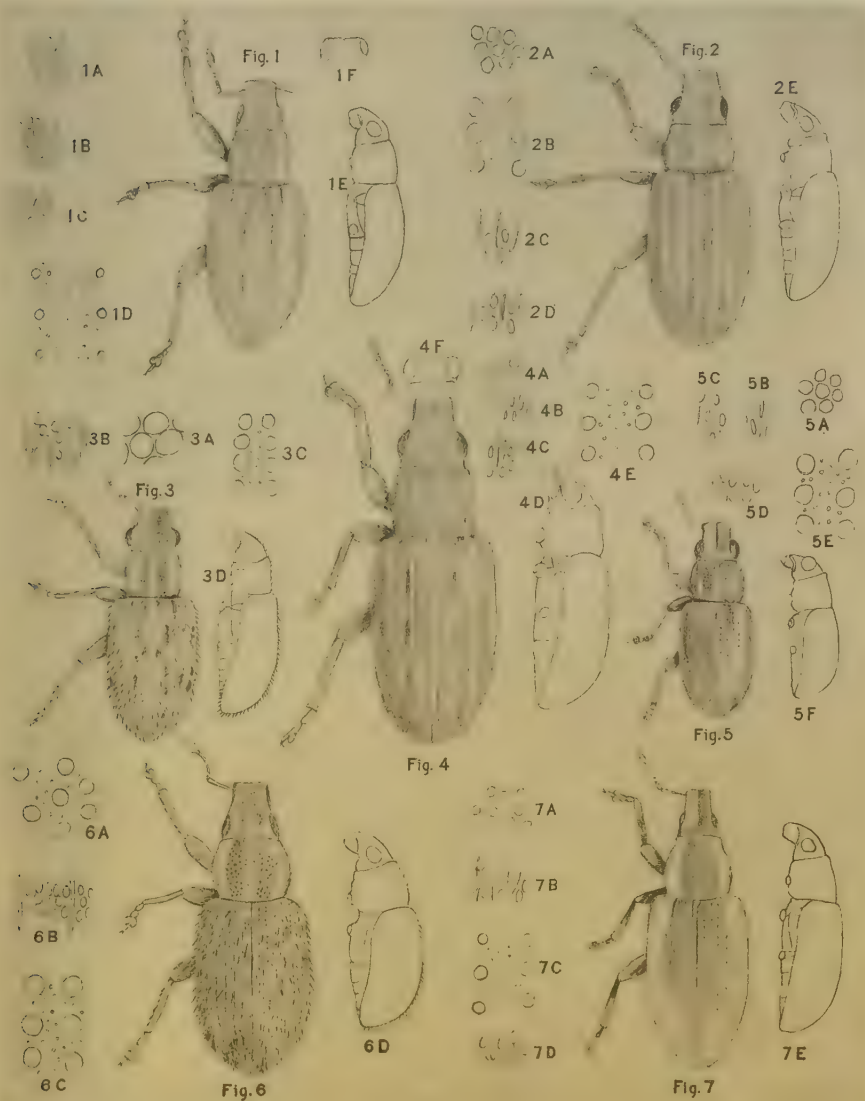
INTRODUCTORY.

It is well known that weevils of the genus *Sitones* are serious pests of leguminous crops throughout the world. Their depredations have been recorded on every species of clover, on vetches, lucerne, peas, beans and lupins. The adults injure the plants by eating the leaves, and crops of peas and beans in their early stages are often destroyed in this manner.

Further damage is also done to the plant by the larvae which feed upon the roots. In the case of peas and beans the larvae are especially destructive to the root nodules which are of such value to the plant on account of the nitrogen fixing bacteria which they contain.

In Great Britain there are several injurious species of *Sitones*. The damage done by *S. lineatus* has been fully related by Miss Ormerod in her *Reports on Injurious Insects* (11) but of the regular though less striking toll effected by many of the other species on clover fields throughout Great Britain much less is known.

Examination of the existing literature on *Sitones* revealed the fact that despite the wide distribution and the destructive habits of these insects, the life-history of no single species in Great Britain was completely known, not even that of *Sitones lineatus*. Many records and observations on *Sitones* were collected by Miss Ormerod, but unfortunately in the majority of cases no attempt was made to establish the identity of the species to which the information referred, with the result that one can gain from her *Reports* very little definite information on any one particular species. As a thorough knowledge of the life-history of a pest is essential to its successful control the genus *Sitones* appeared to me to offer a field for investigation. I have therefore attempted to



Del. D. J. Jackson

Weevils of the genus *Sitones* injurious to Leguminous crops in Britain $\times 8\frac{1}{2}$.

- Fig. 1. *S. flavescens* Marsh. 1 A=punctuation of thorax, 1 B=scales of thorax, 1 C=scales of elytra, 1 D=punctuation of elytra, 1 E=side view of weevil, 1 F=forehead viewed from above.
- Fig. 2. *S. lineatus* L. 2 A=punctuation of thorax, 2 B=punctuation of elytra, 2 C=scales and setae of thorax, 2 D=scales and setae of elytra, 2 E=side view of weevil.
- Fig. 3. *S. crinitus* Herbst. 3 A=punctuation of thorax, 3 B=scales and setae of elytra, 3 C=punctuation of elytra, 3 D=side view of weevil.
- Fig. 4. *S. puncticollis* Steph. 4 A=punctuation of thorax, 4 B=scales and setae of thorax, 4 C=scales and setae of elytra, 4 D=side view of weevil, 4 E=punctuation of elytra, 4 F=forehead viewed from above.
- Fig. 5. *S. sulcifrons* Thunb. 5 A=punctuation of thorax, 5 B=scales and setae of thorax, 5 C=scales and setae of elytra, 5 D=scales from sides of body, 5 E=punctuation of elytra, 5 F=side view of weevil.
- Fig. 6. *S. hispidulus* F. 6 A=punctuation of thorax, 6 B=scales and setae of elytra, 6 C=punctuation of elytra, 6 D=side view of weevil.
- Fig. 7. *S. humeralis* Steph. 7 A=punctuation of thorax, 7 B=scales and setae of thorax, 7 C=punctuation of elytra, 7 D=scales and setae of elytra, 7 E=side view of weevil.

3-4 mm., elytra rather short and broad, widest across the middle and narrowed anteriorly *S. lineellus* Gyll. and *S. tibialis* Herbst. (= *brevicollis* Brit. Cat.).

iii. Elytra without upstanding setae.

1. Dorsal portion of elytra without scales but entirely clothed with fine flat hairs or setae. Size comparatively large, 5-6 mm.; thorax with very large punctures and the sides strongly rounded and dilated *S. cambricus* Steph.
2. Dorsal portion of elytra more or less completely covered with scales interspersed with flat hairs of setae which are rarely absent.

A. Elytra with the sides almost straight, parallel and not becoming wider behind the shoulders, and with the dorsal area when viewed sideways only slightly curved.

a. Width of head across eyes almost equal to width of pronotum.

aa. Elytra moderately long, with distinct, moderately long, almost flat setae evenly distributed amongst the scales and not arranged in groups, pronotum comparatively short, rostrum with central dorsal groove continued between the eyes, size 4-5 mm.

**S. lineatus* L. (Fig. 2).

bb. Elytra shorter, setae shorter and principally arranged irregularly in groups, pronotum comparatively longer, central groove of rostrum not continued between the eyes. Size 6 mm.

**S. puncticollis* Steph. (Fig. 4).

b. Width of head across eyes distinctly narrower than width of pronotum. Head deeply excavated between the eyes. Shoulders usually with a conspicuous patch of pale scales **S. humeralis* Steph. (Fig. 7).

B. Elytra with the sides more or less rounded and the greatest width near the middle, and with the dorsal area distinctly curved when viewed sideways.

a. Head not excavated between the eyes but with a central groove, size 4 to 5½ mm.

aa. Scales ochreous or ochreous brown, thorax very finely and shallowly punctured **S. flavescens* Marsh. (Fig. 1).

bb. Scales coppery red or metallic greenish, punctures on thorax fine but coarser than *flavescens*

S. suturalis Steph. (and var. *ononides* Sharp).

b. Head deeply excavated between the eyes; size small, 2½-3 mm., elytra sparingly covered with scales; a conspicuous patch of white scales on the sides of the thorax and anterior abdominal segments

**S. sulcifrons* Thün. (Fig. 5)

I propose to deal in detail with the species *seriatim* taking first *S. lineatus* to which the remainder of this paper is devoted.

SITONES LINEATUS L.

In 1761 this species was described by Linnaeus(1) who records it as being common in gardens and fields. It is now a well-known pest of leguminous crops and is widely distributed throughout Europe. It is

common throughout the British Isles but is less destructive in the north of Scotland than in the south of England.

FOOD-PLANTS.

Peas, beans, lucerne (*Medicago sativa*), medick (*Medicago lupulina*), all species of clover (*Trifolium*), tares (*Vicia sativa*), and wild vetches.

In Britain this is the most abundant species infesting peas and beans and is only too well known in consequence. I have noticed that it greatly prefers peas, beans and vetches to clover, thus wild vetches growing in fields of clover are often almost denuded of leaves by this species while the clover growing round it is not touched. Similarly comparatively few specimens are to be taken in clover fields if peas and beans are growing in the vicinity, though from October until April this species is common upon clover. On the other hand I have found this species abundant on lucerne throughout the year. It would thus appear that clover is not the favourite food-plant of this species but only resorted to when the others are unobtainable. This view is further supported by examination of the life-history which seems to be specially adapted to peas and beans, as egg laying only takes place during spring or summer when the peas and beans are in a condition to support the resultant larvae.

Other recorded food-plants. E. M. Vassiliev in *Ent. Section of the Rep. of the Exp. Ent. St. of all Russ. Soc. of Sugar Refiners* for 1914, Kiev, 1913, pp. 12-23. *Abstract Rev. App. Ent.* A. 1 (1913), pp. 485 and 487, mentions the occurrence of *S. lineatus* on vines and sugar-beet, though he records it as not a pest of the latter: A. Tullgren in "Skadedjur i Sverige Åren 1912-1916" (Injurious Animals in Sweden during 1912-1916), *Meddelande från Centralanstalten för Jorshruksförsök*, No. 152, *Entomologiska afdelningen*, No. 27, p. 104. *Abstract Rev. App. Ent.* vi (1918), p. 147, observes that *S. lineatus* damages raspberries: E. Molz and D. Schroderas record an attack of *S. lineatus* on chicory and mentions beet being damaged by the larvae. Bargagliolo records as food-plants of this species *Ilex aquifolium* and *Pinus sylvestris*: the latter tree is also recorded by Taschenburg¹² as a habitat of *S. lineatus* but I have no doubt that the weevils were merely sheltering in these trees. I have met with no corroborative evidence of *S. lineatus* occurring on vines, raspberries, chicory or sugar-beet in this country.



Fig. 1. Root of bean plant, showing larvae of *Sitones lineatus* feeding on root nodules.
Fig. 2. Bean plants with leaves damaged by adult of *S. lineatus*.
Fig. 3. Pea plant ditto.

NATURE OF DAMAGE.

I. *Damage by Adult.* (Plate XV, figs. 2 and 3.)

The adult weevils do principal damage to peas and beans when the plants are from 3 to 6 inches high. They feed upon the leaves in a characteristic way. Commencing always at the edge of the leaf they eat U-shaped notches out of it. In the young leaves which are still folded they do the same, thereby forming a notch on each side of the leaf. These notched leaves are typical of the first appearance of the weevil and this stage of the attack is illustrated in the accompanying figures. If many weevils are present and especially if the growth of the plant is at all checked through cold or drought the young leaves and growing shoots are more or less completely eaten away thereby causing great reduction or complete loss of the crop. Miss Ormerod states many instances of farmers having to plough up their pea crops on this account, and the Board of Agriculture⁽²²⁾ records the complete destruction of pea and bean crops in many places during 1917, through the severe attack of this pest.

II. *Damage by Larvae.* (Plate XV, fig. 1.)

The damage effected by the larvae consists chiefly in attacks on the root nodules of peas and beans. This destruction attains its maximum at the commencement of the flowering season. The nodules in all stages of growth are excavated by the larvae and although new nodular growths often develop these also are destroyed by the larvae. After a severe attack only the hollowed out shrunken skins remain; and the nodules are thus often completely destroyed at a critical stage of the plants' development.

Description of Adult. (Plate XIV, fig. 2.)

Black, clothed on the dorsal surface with brownish ochreous or greyish ochreous scales interspersed with flat setae, frequently arranged on the elytra in the form of darker and lighter longitudinal stripes. Under-surface covered with whitish grey scales. Size 3.6 to 5.4 mm.

Build. Head moderately broad between the eyes which are slightly prominent, projecting beyond the line of the sides of the anterior part of the pronotum. Rostrum with a central furrow which is continued between the eyes, but the area between the eyes traversed by the furrow is otherwise level. Pronotum broader than long, the sides rounded, the anterior edge very slightly raised so as to form a narrow rim or collar. Elytra long and with parallel sides, not increasing in width behind the

shoulders but continuing of equal width for two-thirds of their length, then gradually tapering towards the extremity which is oval. The shoulders are moderately prominent. When viewed from the side the elytra are seen to be almost level along the back.

Pubescence and sculpturing. The pronotum is covered with medium sized punctures rather closely placed. It bears numbers of pale coloured setae, the points of which are directed anteriorly and only very slightly raised. These setae increase in size towards the anterior margin of the pronotum. Sparingly distributed amongst the setae are scales which vary in colour in the different specimens, being reddish ochreous, brownish ochreous or greyish ochreous. These scales are larger and more closely placed in a line along the middle and on a broader band on either side, thus giving rise to light dorsal and sub-dorsal stripes. The scales are moderately large, spatulate and forwardly directed.

The elytra have distinct punctured striae, the interstices being marked by very minute sculptured dots. The elytra are closely covered with scales similar to the pronotum but backwardly directed. The scales are of varying colours and are frequently arranged in alternate stripes of light and dark, silvery grey or silvery ochreous. Evenly interspersed with the scales are light coloured setae, flat, and backwardly directed; but becoming longer and slightly more raised towards the extremity of the elytra. These setae are paler and more conspicuous on the alternate striae corresponding with the colour of the scales forming the light coloured stripes.

The sides and under-surface of the body are clothed with whitish grey scales which are frequently tinted with pink. They are larger than those on the dorsal surface and of various shapes and are interspersed with flat setae on the sternites of the thorax and abdomen.

The legs. The femora are black but reddish at the base and extreme apex, clothed with pale ochreous scales and long pale setae, the tibiae and tarsi are light brownish red clothed with long white setae.

The antennae are rather long and slender, brownish red with fine pale hairs.

EXTERNAL SEXUAL DIFFERENCES BETWEEN MALE AND FEMALE.

The sexes can be distinguished by examination of the posterior abdominal segments. The differences are most apparent when the elytra and wings have been removed, but it is possible to differentiate live specimens by examination of the ventral surface only. On the dorsal surface of the abdomen in both sexes eight tergites are present. The

seventh abdominal tergite is known as the propygidium, the eighth as the pygidium. In both sexes the propygidium bears short bristles posteriorly whilst the pygidium is covered with them. The preceding tergites are devoid of bristles. On the ventral surface of the abdomen in both sexes are five visible sternites. According to Hopkins' account¹ of the sternites of beetles of the genus *Dendroctonus* these five sternites may be taken to represent sternites 3 to 7, as the first and second are stated by him to be obscured by the coxal cavity and probably this explanation holds good for *Sitones* also. The area on the sides between the tergites and sternites is occupied by the pleurites. These consist of a more dorsal line of membranous pieces, the epipleurites, which contain the spiracles, and below them a line of chitinous pieces called the hypopleurites. The pleurites are normally covered by the elytra. The external sexual differences are to be found in the shape of the pygidium and the hypopleurites and sternite of the last segment.

The Male. (See Fig. II², IV and VI, p. 276.)

The pygidium is much larger than in the female and completely overlaps the ends of the hypopleurites of each side. The hypopleurite of the last segment is shorter than in the female and ends abruptly where it touches the pygidium and is not continued round the end of the body as a narrow edge dorsal to the sternite. The sternite of the last segment has the edge truncated and not rounded. This point must be examined carefully, for if hastily viewed with a lens the extremity of the sternite of the male often appears as round as that of the female owing to the rounded edge of the pygidium being closely applied to the sternite more or less obliterating the anal orifice which occurs between them.

The anal opening occurs between the pygidium and the seventh sternite.

The Female. (See Fig. I², III and V, p. 276.)

Pygidium much smaller than in the male and not overlapping the hypopleurite. Hypopleurite of the last segment longer than in the male, not ending abruptly but gradually narrowing to a small ridge which is continued round the end of the body above the seventh sternite to join with the hypopleurite of the other side. Seventh sternite with the extremity evenly rounded. Anal orifice occurring between the pygidium and the ridge of the hypopleurite.

¹ "The Genus *Dendroctonus*," by A. D. Hopkins, *U.S. Dept. Agric. Bur. Ent. Technical Series*, No. 17, *Bulletin* No. 83, Part 1, June 1909.

² To simplify these illustrations I have omitted scales, bristles and sculpturing.

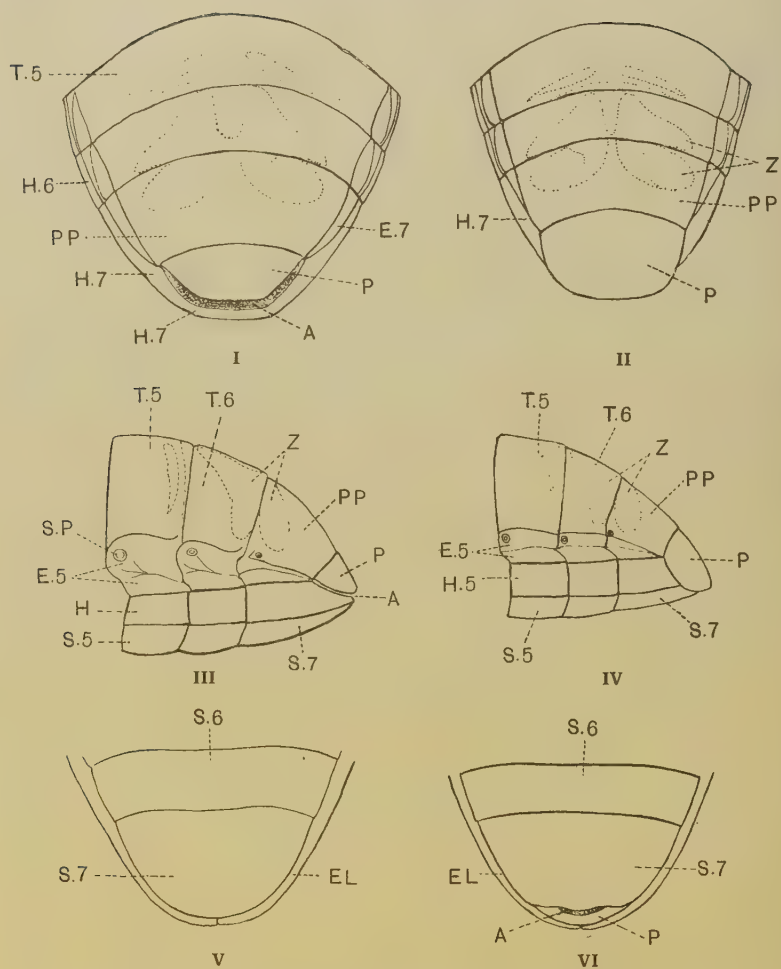


Fig. 1. Posterior abdominal segments of weevils of *S. lineatus* $\times 31$.

- I. Female viewed dorsally with elytra removed.
- II. Male viewed dorsally with elytra removed.
- III. Female viewed laterally with elytra removed.
- IV. Male viewed laterally with elytra removed.
- V. Female viewed ventrally.
- VI. Male viewed ventrally.

A = anus; E = epipleurite; EL = elytra; H = hypopleurite; P = pygidium; S = sternite; SP = spiracle; T = tergite; Z = pubescent area. The numbers following the letters refer to the segments, e.g. T. 6 = tergite of 6th segment.

Sexual differences in the legs. A very slight difference occurs between the legs of the male and female. In the male there is a small pointed prominence at the apex of the tibiae of all the legs on the inner side, but it is most conspicuous on the anterior tibiae. In the female though a slight prominence occurs on the same place it is much smaller on all the legs than in the male. As in both sexes the apex of the tibia is much obscured by long bristles this difference is difficult to ascertain in uncleared specimens and I merely mention it as the presence of a "hook" on the anterior tibiae of the male is given by Fowler (15) as a character for distinguishing the male of this species.

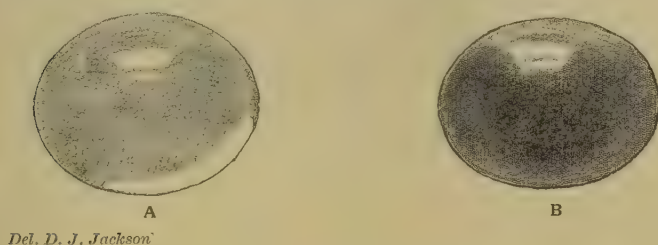


Fig. 2. Eggs of *Sitones lineatus* L. $\times 91$.

A = newly laid egg.

B = egg a few days later.

The Egg. (Fig. 2.)

The eggs viewed with a lens are smooth, but under a microscope their surface is seen to be slightly roughened. In shape they are oblong oval but they vary somewhat in shape as well as in size, some being more spherical than others. The majority measure 0.36 mm. by 0.29 mm. but they are sometimes as large as 0.37 mm. by 0.31 mm. or as small as 0.32 mm. by 0.3 mm. The first eggs laid by the newly mature female are of peculiar shape, being extremely elongated and pointed at both ends, measuring 0.46 mm. by 0.19 mm. When first laid the eggs are yellowish white but they change in two or three days through grey to black.

The Larva. (Plate XVI.)

The larva is legless, but the tenth segment forms a fleshy prominence which is used in walking and is capable of being extended or withdrawn. When full grown the larva measures about $6\frac{1}{2}$ mm. Its

body is cylindrical in shape and tapers slightly towards the extremities. It is usually bent in a curve. It is creamy white in colour, soft and fleshy, and there are many transverse wrinkles on the back dividing the segments up into folds. These folds bear various reddish brown bristles which are constant in number and position in this species. The head is comparatively small, measuring 0.635 mm. long by 0.62 mm. broad. The frons and epicranium are deep ochreous in colour, becoming darker in colour towards the epistome which is reddish chestnut. The jaws are prominent, dark reddish brown. The antennae are extremely small, two jointed. There are no eyes. The body is divided into segments, of which there are three thoracic and ten abdominal, but the last abdominal segment is very small. Along the side of the body is a conspicuous longitudinal fold, the epipleural fold, above which the spiracles

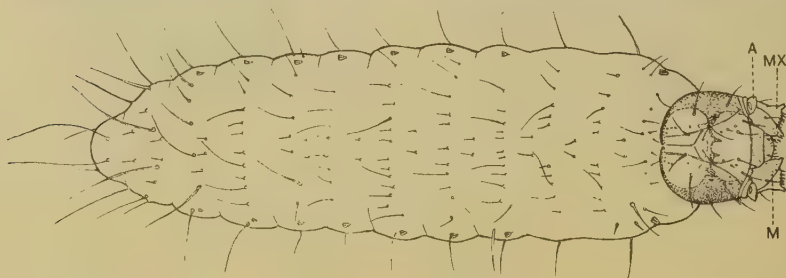


Fig. 3. Newly hatched larva of *Sitones lineatus* L. Dorsal view $\times 94$.

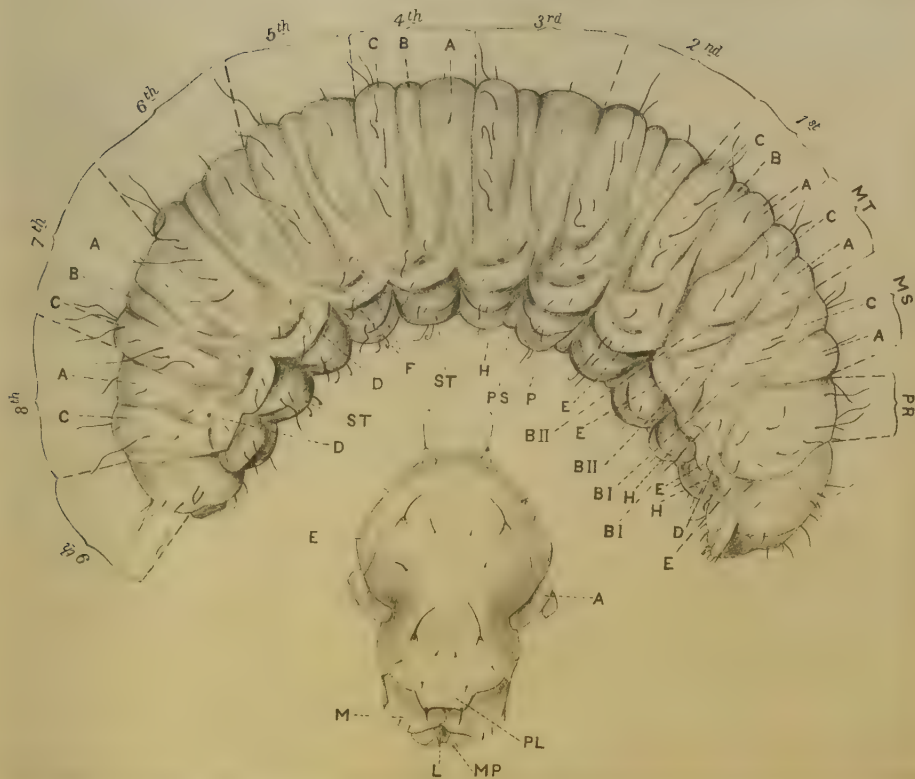
A = antenna; M = mandible; MX = maxilla.

are situated. The spiracles are nine in number; the first pair is situated between the prothorax and the mesothorax, the remainder are situated on the abdominal segments 1 to 8.

It is intended to give a more detailed description of this larva in a subsequent paper dealing with the comparative anatomy of the larvae of the injurious species.

The Newly Hatched Larva. (Fig. 3.)

The newly hatched larva differs from the adult larva in the following points. It is much more active and quick in its movements. Its bristles both on head and body are proportionately very much longer and increase greatly in length towards the end of the body. Their arrangement appears to be much the same as in the adult, but the lobes of the body on which they occur are not clearly represented. The spiracles are comparatively large and situated in the same position as in the adult. The



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Adult larva of *Sitones lineatus* L., lateral view $\times 27\frac{1}{2}$.

A=prescutal lobe; B=scutal lobe; BI=scutal lobe of mesothorax; BII=scutal lobe of metathorax; C=scutellar lobe; D=spiracle; E=epipleural lobe; F=basal portion of scutal fold; H=hypopleural fold; MS=mesothorax; MT=metathorax; P=pleural groove; PS=post sternellar fold; ST=sternellar fold; PR=prothorax; 1st to 9th=1st to 9th abdominal segments.

Head of pupa of *Sitones lineatus* $\times 27\frac{1}{2}$. (Inset)

A=basal portion of antenna; E=eye; L=labium; M=mandible; MP=maxillary palp; PL=pseudo-labrum or epistomal bristle pad.

head differs in colour from that of the adult. The sides of the epicranium and the genae or cheeks are dark brown, as is the gular plate. The frons and the dorsal part of the epicranium being colourless and transparent, these ventral parts appear conspicuously through the dorsal surface. The dark brown area is continued as a narrow strip round the posterior edge of the epicranium. The mandibles and epistome are very light ochreous brown. The antennae are relatively very much larger as compared with those of the adult larva. As in the adult, no eye spots are present. Measurements of the newly hatched larvae are as follows: length of body including head, 0.97 mm. to 1.1 mm.; breadth of body, 0.279 mm.; length of head, 0.182 mm. to 0.198 mm.; breadth of head, 0.163 mm. to 0.173 mm.

The Pupa. (Plate XVII. *Head of Pupa*, Plate XVI.)

The pupa is soft, very easily crushed, creamy white in colour, with more or less conspicuous bristles upon the dorsal surface. It varies in length from under 4 mm. to over 5 mm. The head is bent beneath the prothorax and is therefore not visible when the pupa is viewed dorsally, only the two prominent bristles upon the vertex, and the distal portion of the antennae, curled round at the sides of the pronotum, being apparent. The head bears three pairs of prominent capitate bristles, each ending in a hooked point, the larger ones arising from distinct conical swellings, and some pairs of smaller bristles are also present. The pronotum is provided with a number of moderately long bristles of which the majority are non-capitate. The mesotergum bears on either side of the middle a group of four bristles, some of which are swollen at the tip. Occasionally there are two short bristles anterior to these groups situated one on each side of the median line. The metatergum bears a somewhat similar group of three to four bristles and has occasionally two bristles anterior to these as on the mesotergum. The bristles on the thoracic segments arise from slight elevations. There are ten abdominal segments, the tenth being extremely small and the first eight bear bristles which are arranged in the form of a single transverse row on the posterior portion of each segment. They are much shorter than the bristles of the thorax and slope towards the posterior extremity of the body. They are borne upon distinct paplike elevations, which become more marked on the posterior segments. The number of bristles upon the abdomen vary in different specimens but on segments 1-7 the number is usually eight, made up of one pair of dorsal bristles, two pairs of lateral bristles, and one pair of pleural bristles, but in some specimens there are six more

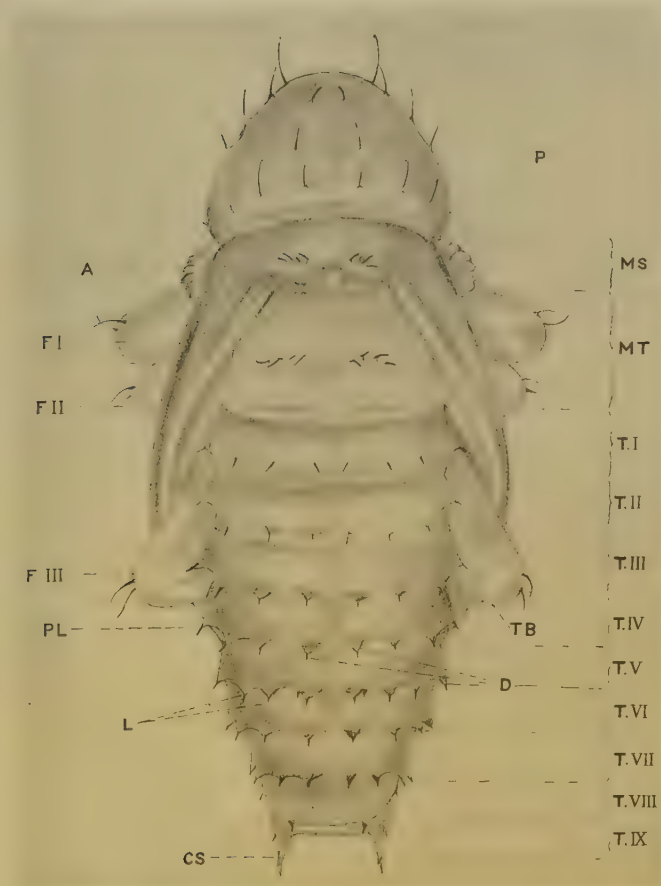
smaller bristles on each segment, one occurring on each side between the dorsal and lateral bristles, another between the lateral bristles and one beside the pleural bristle. The eighth segment bears only one bristle-bearing pap on each side, the ninth terminates at each corner in a large and prominent spinous process which is covered especially posteriorly with numbers of minute pointed projections and bears on either side a backwardly directed spine. The tenth segment is visible on the ventral surface, between the spinous processes of the ninth segment. It consists of two lobes, representing tergite or supra-anal lobe and sternite or infra-anal lobe. The spiracles of the abdominal segments are situated on the sides in the region of the pleural bristles. The femora of the legs project prominently from the sides of the body, and each one bears at its extremity a pair of conspicuous hooked and capitate bristles.

EXTERNAL SEXUAL DIFFERENCES BETWEEN THE MALE AND FEMALE PUPAE.

The male and female pupae can be distinguished by examination of the posterior abdominal segments. The tergites, pleurites and sternites so clearly marked in the adult weevil can be traced in the pupae of both sexes as areas separated by ridges or incised lines. The abdominal tergites in the pupa comprise the region of the back occupied by the dorsal and lateral spines; the epipleural region containing the spiracles is indistinctly distinguished from the tergal region by an undulating ridge more conspicuous on the posterior segments. It bears dorsally the pleural spines. The hypopleurites can be easily recognised as flat areas on the sides below the epipleurites, and the ventral surface is occupied by the sternites. The external sexual differences are to be found in the shape of the seventh sternite and the eighth tergite.

The Male. (Fig. 4, A and B.)

The male pupa has the surface of the sternite of the seventh segment flat or only very slightly rounded; its outline when viewed from the side (Fig. 4, A) not projecting beyond the surface of the sternite of the eighth segment. The posterior edge of the seventh sternite where it meets the eighth sternite is almost quite straight and bluntly angulated at the junction of the hypopleurite of each side (Fig. 4, B). The tergite of the eighth segment is also longer and larger than in the female and its surface is flatter.



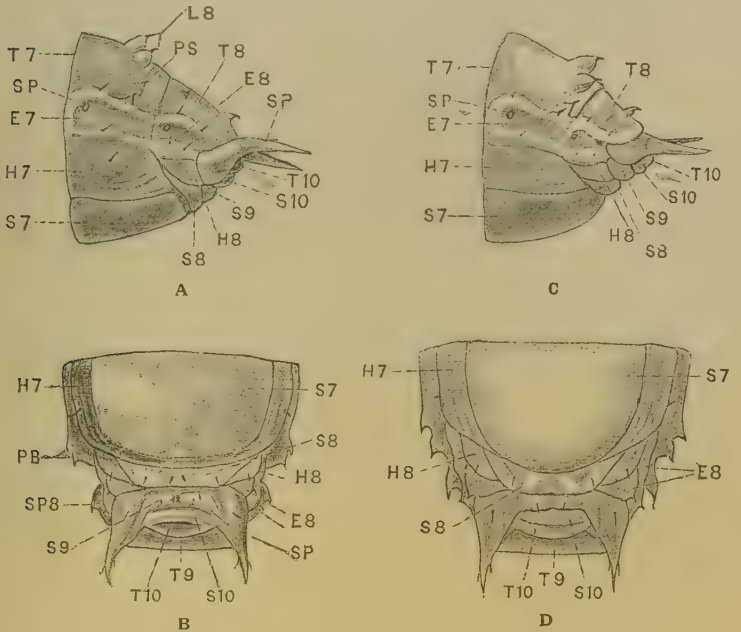
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Pupa of *Sitones lineatus* L. Dorsal view $\times 27\frac{1}{2}$.

A = antenna; CS = caudal spine; D = dorsal spines; F I = femur of 1st pair of legs; F II = femur of 2nd pair of legs; F III = femur of 3rd pair of legs; L = lateral spines; MS = mesotergum; MT = metatergum; P = pronotum; T. I-T. IX = 1st to 9th abdominal tergites; TB = tibia of 3rd pair of legs.

The Female. (Fig. 4, C and D.)

The female pupa has the surface of the sternite of the seventh segment more convex posteriorly than the male, so that its outline when viewed sideways is strongly curved posteriorly and projects prominently beyond



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Fig. 4. Posterior abdominal segments of pupae of *Sitones lineatus* L. showing sexual differences $\times 35$.

A. Male, lateral view.

C. Female, lateral view.

B. Male, ventral view.

D. Female, ventral view.

E = epipleurite; H = hypopleurite; L.S. = lateral spines; P.S. = pleural spines; S = sternite; S.P. = spinous process; T = tergite. 7, 8, 9 and 10 = 7th, 8th, 9th and 10th segments.

the surface of the eighth sternite (Fig. 4, C). The posterior edge of the seventh sternite is also strongly and evenly rounded posteriorly (Fig. 4, D). The seventh tergite is much shorter than in the male with the surface less flat.

LIFE-HISTORY.

SUMMARY OF LIFE-HISTORY IN BRITAIN AS AT PRESENT KNOWN.

The most recent observations on the life-history of *S. lineatus* in Britain occur, as far as I have been able to discover, in Miss Ormerod's *Reports* from the year 1878 to 1892. They may be thus briefly summarised. Weevils of *S. lineatus* issuing from their winter quarters were known to attack peas and beans in spring. These beetles laid eggs, and larvae of this species were observed by Hart at the roots of peas in the end of May. Weevils emerged from these during July. Sitones weevils continued to be abundant on the peas until the time of harvesting, and in autumn adult Sitones were to be found in abundance amongst clover stubble. Sitones larvae were also to be found in great abundance at the roots of clover from November to May and adults emerged from these in June. As this observation is placed under the heading of *Sitones puncticollis* some at least of the weevils reared from these larvae must have been of this latter species.

Miss Ormerod's conclusions from these observations are that the weevils of *lineatus* after hibernation attack peas in spring, and produce there another generation which emerges in July; that in June the weevils developed from larvae which have spent the winter at the roots of clover, join the swarms on peas, and at the time of harvesting the peas all the weevils migrate to clover fields and a portion hibernate, but the remainder lay eggs which give rise to larvae that feed on clover roots throughout the winter.

From this one would understand that there is a partial second generation of the pea-feeding weevils at the roots of clover, but whether this generation is produced by the original hibernated weevils (in which case it would not be in the true sense a second generation but only a later brood of the same parents), or by their descendants, or by the weevils that emerge from clover in June, is left in doubt. My researches show that the life-history of two or more species have here been confused, as the larvae which occur at the roots of clover in winter are not those of *S. lineatus* but belong to other species, the life-history of which I intend to deal with in subsequent parts of this paper.

SUMMARY OF THE LIFE-HISTORY AS I HAVE FOUND IT.

In the beginning of the year, from January until March or April, the adult weevils remain in their winter quarters, sheltering amongst long grass, in stacks of pea straw, amongst the stubble of clover fields,

or even lying more or less exposed on the earth between the plants. In the first warm days of spring the majority migrate to peas and beans, only a very few remaining upon the clover. They very soon commence to lay eggs, and egg laying continues until shortly before the death of the parent weevil, in the south of England at the end of June or the beginning of July, and in the north of Scotland in August or the beginning of September. I have never observed the adults live through a second winter. The eggs hatch in 20 to 21 days and the young larvae become mature in about six or seven weeks. The pupal stage lasts about three weeks. The emergence of weevils is thus spread over several weeks commencing in England in July, in Scotland in August. All the weevils, however, emerge before the winter except in rare cases in the north of Scotland, when belated specimens are to be found in the pupal stage in mid-winter. The newly emerged weevils are sexually immature, the ovary of the female being quite undeveloped and maturing very slowly so that egg-laying does not commence till the following spring. The few weevils that remain upon clover throughout the summer oviposit similarly and their progeny develop in the same way, as I have proved experimentally. There is thus only one generation in the year.

DETAILED OBSERVATIONS ON LIFE-HISTORY AND HABITS.

As already mentioned the winter is passed in the adult stage. I will therefore commence to follow the life-history in detail from the time when the weevils make their appearance upon the peas and beans in spring, and will give an account of the field observation and breeding experiments upon which my conclusions rest. The field observations have been made at Wye, Kent, and in Ross-shire, and as differences occur in the time of appearance of the weevil in its different stages in these widely separated localities, I here record them. The breeding experiments have been carried out principally in Ross-shire. For this purpose flower pots were used in which the food-plant had been previously grown from seed, the pots being kept in a glasshouse to prevent the access of "wild" *Sitones* before the commencement of the experiments. A large wire ring was then attached horizontally to sticks thrust in the soil at the sides of the pot and the whole sleeved with muslin, the wire ring preventing the muslin from touching the leaves of the plants (Plate XVIII, fig. B). These pots were always kept out of doors and proved most useful for observing details of the life-history. With the object of carrying out control experiments under even more natural conditions, I had large breeding cages constructed 3 feet square with

wooden sides about 1 foot high, and a frame above covered with muslin or finely perforated zinc. These cages were made without bottoms and the wooden sides were sunk in the earth, thus preventing any of the larvae from escaping and providing the plants with abundance of air and light. Admittance is obtained through sleeves let into the muslin, or, when perforated zinc is used, by a movable lid. In the photograph (Plate XIX) four of these cases are seen in position while the fifth is awaiting the process of digging in.

The hibernated weevils. The serious damage to peas and beans is done by the hibernated weevils in spring. The date of their appearance on these plants in spring varies according to the season and the latitude. In Kent, in 1918, the spring was normal, and I noted the weevils on the field peas for the first time on March 27th. In 1919 the season was very backward and I found no weevils until April 8th, and the majority did not appear till the middle of that month. In the north of Scotland, in 1919, the peas were not up till the beginning of May, and by the middle of that month weevils were abundant on them. Early in spring when the weather was cold the weevils were to be found in the daytime hiding under lumps of earth near the base of the plant, and sometimes on the stem of the plant near the root where it was sheltered by clods of earth, but in warm, sunny weather many of the weevils were to be found running about the leaves of the bean plants, or hiding in the leaf axils or between the unopened leaves. I noticed that their method of attack on the foliage of peas and beans differs after a certain stage. On beans the weevils feed principally on the young unopened leaves of the terminal shoots from the time the plant appears above ground till it is ready for cutting. With peas the terminal growing shoots are only eaten whilst the plant is small and not more than a few inches above the ground. When over a foot high the growing shoots are rarely touched and only the leaves near the ground are eaten. I attribute this difference to the greater shelter which the stiffer bean leaves afford to the weevils whilst eating. Large firm leaves, the axils of which form convenient hiding places, surround the young shoots of the broad bean, whilst on peas the young leaves are slenderer, more exposed, and the weevils have to seek shelter and a firmer foothold lower down. With both crops the most serious damage is done by the weevils early in the spring while the plants are still small. The weevils on disturbance immediately feign death and fall from the plant, but after a short pause run quickly under a clod of earth or down a crack, from which position they are not easy to secure. When present on peas or beans under natural conditions I have



Fig. A.

Fig. B.

PLATE XVIII

Fig. A. Pot containing growing clover, as used for observation of egg-laying of weevils, the thick muslin sleeve being fastened round the clover plants above the root.

Fig. B. Pot containing growing clover as used for breeding experiments.



PLATE XIX

Cages used for breeding experiments.

never observed the weevils fly, but in spring if confined in a small space and placed in sunlight they become very active and use their wings freely. If liberated under these conditions they run about for a short time, then raise their elytra, spread their wings and fly quickly out of sight. The hibernated weevils were to be found in Kent until the beginning of July, and from Hampshire I received a hibernated female collected as late as August 11th. In Ross-shire they were to be found till the end of August or the beginning of September, but only a few occurred towards the end of these periods. As the weevils become older they get more rubbed till eventually practically all their scales disappear. They can thus be easily distinguished superficially from their newly-hatched progeny. In captivity weevils collected in Kent in April began to die off in the end of June, but a few survived till August 3rd. From weevils collected in Ross-shire in July a few survived in captivity till the middle of November. None of the hibernated weevils from Kent or Ross-shire were observed to live through a second winter.

Egg-laying. As will be shown later, the weevils do not commence to lay eggs until spring, but in the beginning of April in Kent, in the middle of May in Ross-shire, they lay eggs freely and are frequently to be found paired. At first only a few eggs, one to five, are laid per day, but later sometimes as many as 24 are laid daily. The numbers laid by different females varies greatly; thus one female under observation commenced laying on April 21st and continued laying till the beginning of September, producing in all 354 eggs, but another which commenced to oviposit on May 6th continued to do so till the middle of November, when a total of 1655 was attained. No doubt the confinement in small dishes which these experiments necessitated, together with the abundant food supplied, prolonged the life and the egg-laying activities of these weevils, as in fields even in Scotland egg-laying had ceased in September. A few days before commencement of egg-laying pairing takes place and continues throughout the egg-laying season. The eggs are laid indiscriminately amongst the earth at the base of the plant where the beetles rest, and whilst still pale in colour may often be seen adhering to the under-surface of the clods. The eggs shrivel up unless they are kept damp, but they hatch well if kept in moist earth.

The weevils continue to lay until a short time before their death but fewer eggs are laid towards the end and only a minority of these hatched. In confinement eggs laid at different dates throughout the summer hatched always in 20 or 21 days. The egg-laying period thus extends in

England from the beginning of April to the beginning of July, and in Scotland from the middle of May to the end of August.

The larval period. The young larva escapes from the egg by making an irregular hole at one end, and must then burrow to the roots of the plant, as on May 21st in a field in Kent, I found very young larvae measuring 1 mm. in length inside the nodules of the pea roots some distance below the surface of the ground. The larvae were to be found in a curved position inside the small nodules, but I failed to detect their presence from the external appearance of the nodule, and it was only by opening a large number with a needle that I found them. The larva must enter the nodule when newly hatched by a minute hole which is not easy to trace. I found several nodules with small holes in them but these were emptied of their contents and contained no larvae. When about quarter grown the larvae are to be found feeding freely upon the root nodules. On June 3rd larvae of different sizes were abundant at the roots of peas and beans in Kent, and one had already ensconced itself in an oval cell in the earth preparing for pupation. The larvae were always to be found amongst the root nodules, usually with their body partly buried in them. As many as six to nine larvae often occurred at the roots of a single plant in Kent and the nodules were much destroyed in consequence. By the middle of June in some pea fields in Kent, scarcely any nodules in a healthy condition were to be found on the roots, and the hollowed out ones that remained testified to the working of the larvae. In such cases no young larvae were to be found at the roots, so doubtless when a severe attack has already occurred many of the larvae resulting from later laid eggs will die from lack of food. In the north of Scotland larvae in various stages of growth were common at the roots of beans in the end of June, and full fed larvae were common on July 24th. Full grown larvae and even a few half-grown ones were still to be found in this locality on September 2nd, but the majority by this time were in the pupal stage.

Field observations would roughly indicate that the time taken for the growth of the larva from hatching till pupation does not exceed six or seven weeks, judging from the fact that in Kent the weevils commenced egg-laying in the beginning of April (the eggs taking three weeks to hatch), and the first pupa in the same locality was observed on June 10th. To determine the duration of the larval period more exactly, I carried out the following experiment in Scotland in one of the large breeding cages already described, in which peas had been grown from seed. I placed in this a large number of eggs laid between the 25th and

28th May. By July 23rd some of the resultant larvae were full grown and all were mature by July 31st. The first pupa was found on July 30th, and the remainder pupated between that date and August 6th. As the eggs would commence hatching from 15th to the 18th June this would give a larval period of from 45 to 49 days.

It is interesting to note that even when the species is bred in captivity under the most favourable conditions, only a few larvae survive from the many eggs originally used in the experiment, though sufficient food is present to support many more. As nearly all the eggs hatch when observed in the laboratory, no doubt the greatest mortality occurs amongst the newly hatched larvae (as pointed out by Baranov(17)), owing to lack of food whilst seeking for a root nodule to bore into. Greater difficulty was also experienced in breeding larvae on clover than on peas and beans.

The pupal period. The full fed larva excavates an oval cell in the soil for pupation $\frac{1}{2}$ inch to 2 inches below the surface. In Kent I observed the first pupa on June 10th, and in Ross-shire on July 24th. In the latter locality pupae were abundant during August and still to be found in the beginning of September, whilst on January 17th I succeeded in finding two belated pupae in the soil of the old bean field. These must have resulted from the last laid eggs of the old weevils as the following breeding experiment testifies. On July 24th I placed some egg-laying females from Ross-shire on to a sleeved pot of clover, and on November 19th found a pupa in it which remained in this stage throughout the winter. All these belated pupae died in captivity. The pupal stage normally lasts from 16 to 19 days, but after casting the pupal skin the weevil remains in the earthen cell five or six days until the cuticle hardens and the normal colouring is assumed. About nine days before emergence colour changes may be observed in the pupa. The eyes first become brown, then the mouth parts and the apices of the femora and the tibiae darken, and before emergence the wing cases, face, antennae and legs are brownish grey. When the pupal skin is shed the weevil is entirely pale ochreous, with the head brownish grey, the eyes black and the apices of the femora and the entire tibiae deeper ochreous. The following day the thorax and legs become brownish grey and the elytra later turn greyish ochreous; by the fourth day the colour has become gradually darker, and on the fifth day the normal colour is usually assumed, though in some cases the cuticle is still soft.

The newly emerged weevils. These appear upon the peas and beans in July in Kent, in August in Ross-shire. From Suffolk Mr B. S. Harwood

forwarded me a large number, all newly emerged, collected from beans on July 30th, but observed that earlier in the month no specimens of *lineatus* were obtainable. In captivity larvae collected from pea-roots in Kent on June 5th did not mature to weevils till the end of July and the beginning of August, but I have always found that collected larvae take longer to mature than those left undisturbed. In Ross-shire eggs laid from 25th to 28th May produced weevils towards the end of August. On emergence none of these weevils paired or laid eggs, and in order to see when they would do so under the most natural conditions possible I placed them in sleeves of muslin fastened tightly on to plants of peas or clover growing in pots (Plate XVIII, fig. A). These sleeves have proved very satisfactory, as the black eggs can be clearly seen upon them while they would be difficult to find if laid directly on the earth. The weevils also have plenty of fresh food and air. No eggs were laid by these specimens until the following spring, when on May 23rd the first female commenced oviposition. In the field I collected numbers of newly emerged weevils in Ross-shire in August and September, but none of these laid eggs until May 17th next year. In Kent, in October, I collected hundreds of weevils of *S. lineatus* and kept them under close observation, but not a single egg was laid by them that year. I placed a large number of these specimens on the sleeves described above and left them in Kent under the charge of Mr P. F. Kendall, who forwarded a sleeve to me each month, but none of these English weevils, even when kept in their own climate, laid any eggs until next spring when oviposition commenced on May 6th.

Conclusive proof that the weevils do not lay eggs the same year as they emerge will be shown in dealing with the reproductive organs.

On emergence the weevils commence to feed upon the peas and beans but do little harm as the plants by this time are full grown. When the crop is harvested the weevils mostly disperse and some are carted away with the crops, but a few are to be found in mid-winter on the old fields. I have taken these weevils abundantly on lucerne in Kent in October, also on clover and medick, and a few were present on bean plants that had grown up from fallen seed. In that month I also found numbers sheltering in a stack of pea straw and I took a few specimens again in this stack in the beginning of April. During the winter I have found the weevils sheltering amongst long grass beside which there was no clover. In captivity they thrive well with very little food during the winter. Thus in August I placed 15 specimens upon a pot of peas. The peas died during the winter and the weevils had no subsequent food,

but on May 10th ten of the weevils were alive and active and commenced laying eggs on May 17th.

With the first warm days of spring the weevils leave their winter quarters and migrate to peas and beans and there commence their destructive work.

The length of life cycle of an average individual may be thus summarised: egg 3 weeks, larva 7 weeks, pupa 3 weeks, imago 12 months = Total 15 months.

The months during which the weevil occurs in its different stages in Scotland and England may be tabulated as follows:

	Kent	Ross-shire
Egg Stage	April and May diminishing June	May and June diminishing July
Larval stage	May to beginning July	End June and July diminishing August and September
Pupal stage	June and July	End July to September
Imaginal stage	July to July	August to August

THE REPRODUCTIVE ORGANS OF *SITONES LINEATUS*.

The reproductive organs of the newly emerged weevils are immature, particularly those of the female, which have to develop to four times their original size before egg-laying can take place. The male organs also undergo development but not to the same extent.

Description of the Reproductive Organs of the Mature Male. (Fig. 5, III.)

The male reproductive organs comprise testes, paired vasa deferentia, seminal vesicles, and seminal tubes, unpaired vas deferens or common duct and the internal sac. The latter has the appearance of being more or less surrounded by chitinous parts, consisting of tegmen and median lobe, which in reality form with the internal sac and connecting membranes a continuous tube inverted when not in use.

The *testes* are conspicuous yellow bodies lying one on each side of the body beneath the third, fourth, and fifth abdominal tergites. In their natural position the posterior part of the colon and rectum of the alimentary canal lie between the testes, but are dorsal to the vasa deferentia. Underneath the alimentary canal the struts of the median lobe project between the testes posteriorly. The testes of the mature male measure 1 mm. long by 0.85 mm. broad. Viewed dorsally the testes are oval and lobed in outline but are compressed dorso-ventrally (see Fig. 5, II, T). They are covered by a thin membrane which supports tracheae and strands of fat body, the latter imparting a yellow colour to the testes viewed as a whole.

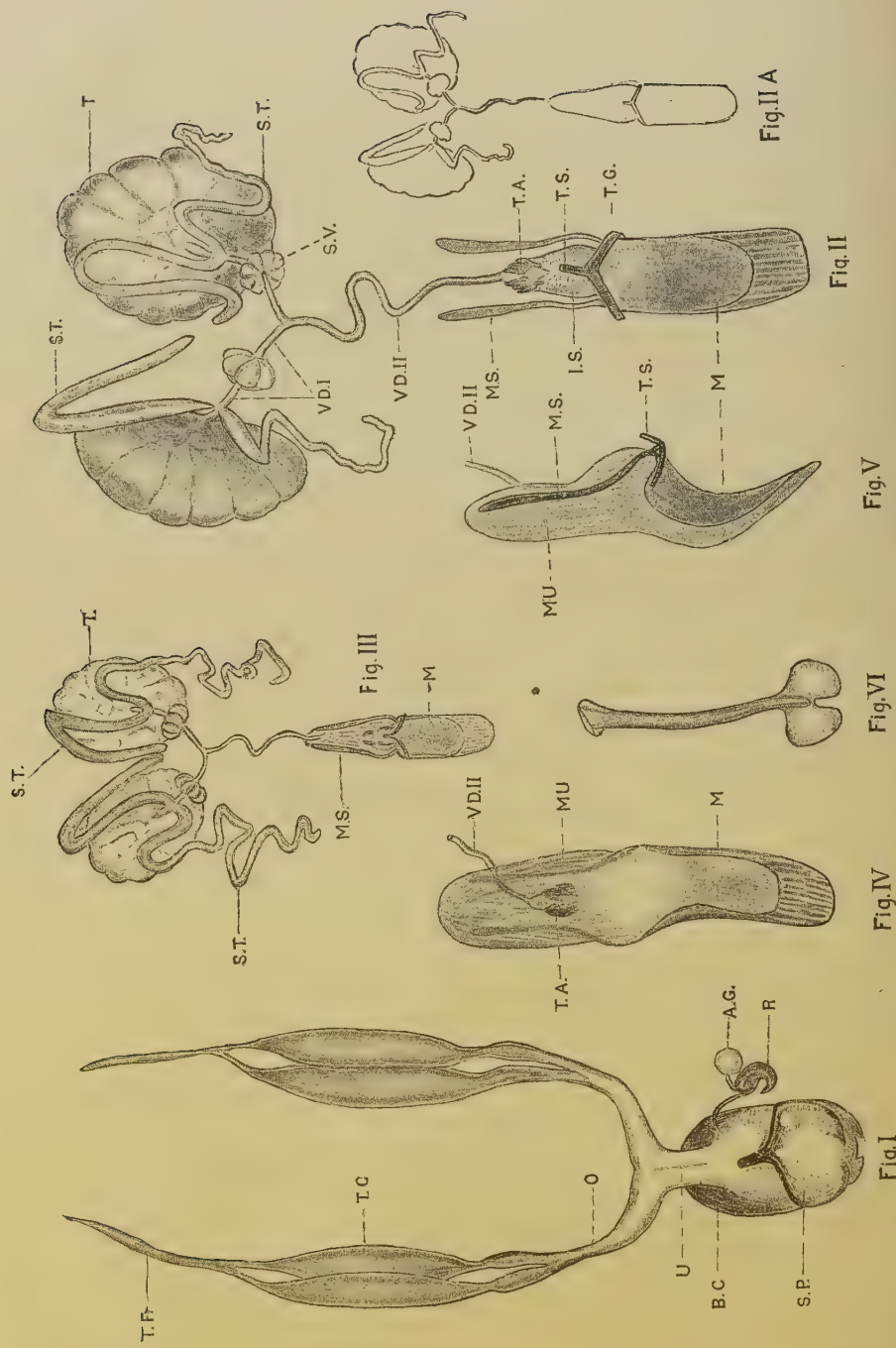


Fig. 5. Reproductive organs of *Sitones lineatus* L. For description of figure see opposite page.

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The paired *vasa deferentia* (Fig. 5, II, V.D.I) consist of a tube leading from the testes of each side to the unpaired vas deferens formed by their junction.

The *seminal tubes* (Fig. 5, II, S.T.) consist of two tubes on each side of the body which open into the paired vasa deferentia very close to the junction of the latter with the testes. These tubes are opaque white in colour and lie closely against the ventral surface of the testes. The inner tube is always more or less elbowed in shape and not convoluted; the outer seminal tube is very long in the mature male and greatly convoluted.

The *seminal vesicles* (Fig. 5, II, S.V.) are two in number, one being present on each side surrounding the paired vas deferens just below the junction of the seminal tubes. It is a transparent bulb-like structure consisting of eight lobes radiating from the centre. In the mature male they measure 0.34 mm. by 0.17 mm. long.

The *unpaired vas deferens* or common duct (Fig. 5, II, V.D. II) is formed by the junction of the paired vasa deferentia a short distance below the seminal vesicle. It is a long tube though when not extended during copulation it is coiled in a very short space. It opens posteriorly into the *internal sac*¹ (Fig. 5, II, I.S.), a membranous structure, the anterior part of which is covered with minute scales of chitin. At the junction of the vas deferens with the internal sac there is a chitinous structure known as the *transfer apparatus* (Fig. 5, II and IV, T.A.). In repose the internal sac is partially withdrawn inside the median lobe, its anterior end projecting between the struts of the median lobe, but when

- I. Reproductive organs of immature female of *Sitones lineatus* L. from one to five months old $\times 37\frac{1}{2}$, ventral view
- II. Reproductive organs of immature male, ventral view, from one to five months old $\times 37\frac{1}{2}$.
- II A. Same but $\times 19\frac{1}{2}$.
- III. Reproductive organs of mature male eight months old as dissected in April $\times 19\frac{1}{2}$.
- IV. Male genitalia, dorsal view $\times 37\frac{1}{2}$.
- V. Same, lateral view.
- VI. Spiculum gastrale of male $\times 37\frac{1}{2}$.

A.G.=accessory gland; B.C.=Bursa copulatrix; I.S.=internal sac; M=median lobe; M.S.=struts of median lobe; M.U.=muscle; O=paired oviduct; R=receptaculum seminis; S.P.=spiculum ventrale; S.T.=seminal tubes; S.V.=seminal vesicle; T=testes; T.A.=transfer apparatus; T.C.=terminal chamber; T.F.=terminal filament; T.G.=tegmen; T.S.=tegmenal strut; U=uterus; V.D. I=paired vasa deferentia; V.D. II=vas deferens.

¹ The terminology of the genitalia which I here use is that adopted by Dr David Sharp, in his most valuable and helpful paper, "Studies in Rhynchophora," *Trans. of the Ent. Soc. of London*, Dec. 1918, pp. 209-222.

the genital tube is everted during copulation, the anterior end of the internal sac becomes the apex of the tube, and it is on this transfer apparatus that the functional orifice is situated.

The *median lobe* (Fig. 5, II, III, IV and V, M.) has the under-surface and sides chitinous and thus resembles a trough, the sides of which decrease in size towards the apex. It is of characteristic shape in the different species of *Sitones* which I have examined. It bears anteriorly two long chitinous struts which arise from its ventral surface with a pronounced angular curve. Between those struts and partly surrounding them is a mass of longitudinal muscles extending from the median lobe to the apex of the struts. These muscles encircle the apex of the internal sac and the transfer apparatus, and to examine these structures the genitalia have to be boiled in caustic soda to remove the muscles. The median lobe is protruded from the body during copulation but does not enter the genital tube of the female, the internal sac being everted through its apex. The median lobe measures 0.54 mm. long by 0.294 mm. broad, the struts 0.77 mm. long.

The *tegmen* (Fig. 5, II, T.G.), the chitinous part of the tegminal layer which forms the portion of the genital tube connecting with the apex of the abdomen, is represented by a semicircular band of chitin bearing anteriorly a short median strut. The median lobe when not functioning is drawn within the tegmen, so that the latter appears to be situated at its anterior edge on the ventral surface.

The *spiculum gastrale* (Fig. 5, VI) is a slightly curved chitinous rod which occurs beneath the genital tube at the apex of the abdomen. It is a median unpaired structure with the anterior end enlarged and the posterior end expanding into a spatulate disc. It measures 0.961 mm. long.

Development of the Reproductive Organs of Male.

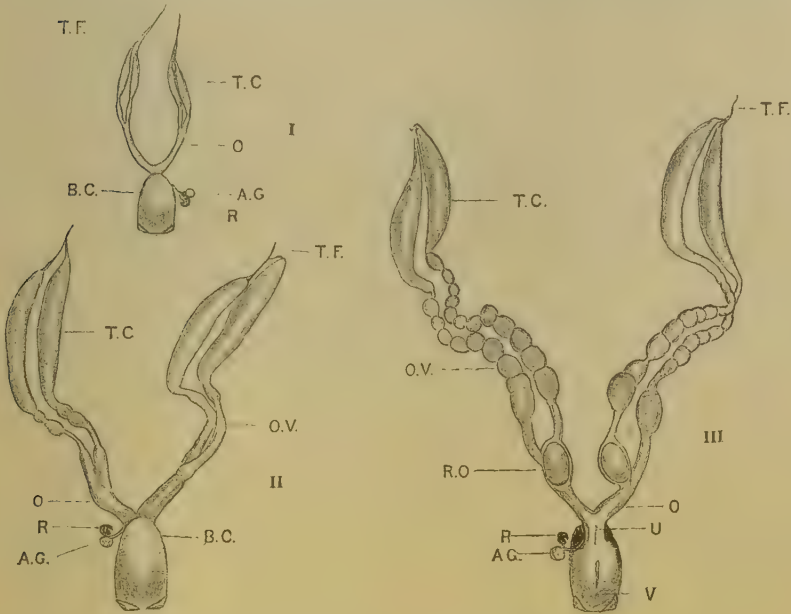
The male of *Sitones lineatus* is mature nine months after emergence in the spring of the year following its emergence. The immature male (Fig. 5, II and II.A) differs from the mature male (Fig. 5, III) in the following respects.

- (1) The testes are smaller, measuring 0.8 mm. long by 0.6 mm. broad.
- (2) The seminal vesicles are smaller, measuring 0.21 mm. broad by 0.13 mm. long.
- (3) The seminal tubes are considerably smaller in size and breadth.

The other parts are the same as in the the mature male. The reproductive organs of the male weevil remain in this condition during the winter but growth commences about March.

*Description of the Reproductive Organs of the Mature Female
at commencement of Egg-laying. (Fig. 6, III.)*

The mature reproductive organs in the female comprise the ovarian tubules, each with a terminal chamber; paired oviducts; unpaired



Del D. J. Jackson

Fig. 6. Reproductive organs of female of *Sitona lineatus* L. showing different stages in development $\times 15\frac{1}{2}$.

- I. Reproductive organs of immature female from one to five months old, as dissected from emergence of weevil in autumn until January, dorsal view.
- II. Reproductive organs of older female—not yet mature—as dissected in March, dorsal view.
- III. Reproductive organs of mature egg-laying female eight months old as dissected in April, ventral view.

A.G. = accessory gland; B.C. = bursa copulatrix; O. = paired oviduct; O.V. = ovarian tubules; R = receptaculum seminis; R.O. = ripe ovum about to be laid; T.C. = terminal chamber; T.F. = terminal filament; U = uterus; V = vagina.

oviduct or uterus; bursa copulatrix; receptaculum seminis and accessory gland. There are four ovarian tubules (Fig. 6, II and III, O.V.), two on each side of the body. Each is composed of a transparent tube enclosing

a row of eggs of gradually increasing size; anteriorly the immature ova are small; but posteriorly, towards the junction of the two egg tubes with the paired oviduct of each side, full-sized mature ova occur. Anteriorly the egg tubes arise from an unsegmented portion called the *terminal chamber* (Fig. 6, I, II, III, T.C. and Fig. 5, I, T.C.). The ends of the two terminal chambers are united by means of the *terminal filament*. The paired oviducts unite after a short course to form the *unpaired oviduct* or *uterus* (U). On the dorsal side of the latter is a large sac, the *bursa copulatrix* (B.C.), which projects at its anterior edge from the uterus but elsewhere is united to it. The *receptaculum seminis* (R) is a small brown chitinous vesicle curved in the form of a hook and united by a slender tube to the uterus at the junction of the bursa copulatrix. A small white *accessory gland* (A.G.) is attached to the receptaculum seminis by a slender tube. The portion of the uterus below the bursa copulatrix is known as the *vagina*. At each side of it posteriorly is a small triangular chitinous plate, and before this on the ventral surface is a medium chitinous rod. A semi-transparent chitinous framework occurs in the ventral wall of the vagina. Attached by muscles to the ventral surface of the vagina is a large chitinous plate known as the *spiculum ventrale* (Fig. 5, I, S.P.).

Development of the Female Reproductive Organs.

On emergence from the pupa in autumn the reproductive organs of the female are exceedingly small and little developed. They remain in this state during the winter but growth commences in March, and by April or May the reproductive organs are mature and eggs are deposited. During spring and summer egg-laying is continued and the ovarian tubules continue to grow, increasing to about twice the size they were at the commencement of egg-laying, and to 12 times the size they were during the winter. Different stages in the growth have been selected, and are described below. Measurements are included to allow of comparison as to the growth of the different parts of the reproductive organs but on account of individual variation they can only be taken roughly.

Immature female, one to five months old (Fig. 6, I, and enlarged Fig. 5, I). In this stage all parts of the reproductive organs are extremely small, and the ovarian tubules show scarcely any development. The paired oviducts are proportionately long, and the terminal filament (arising from the terminal chamber) has attained its full growth. Measurements: ovarian tubule, 0.3 mm.; terminal chamber, 0.49 mm.; uterus and vagina, 0.6 mm.

Immature female, seven months old (Fig. 6, II). By this time considerable growth has taken place and the reproductive organs differ only from those of the female at the commencement of egg-laying in that the ovarian tubules are only one-third the size, and are unsegmented excepting for a small portion anteriorly. Measurements: ovarian tubule, 1.1 mm.; terminal chamber, 1.1 mm.; uterus and vagina, 1.0 mm.

Mature female at commencement of egg-laying (Fig. 6, III). This stage has already been described. Measurements: ovarian tubule, 3.3 mm.; terminal chamber, 1.3 mm.; uterus and vagina, 1.0 mm.

Mature female towards end of egg-laying. By this time the ovarian tubules have increased greatly in length whilst the other parts of the reproductive organs remain the same, the terminal chamber in some cases showing a slight decrease in size. About 20 segmented ova can be counted in each tubule, while the anterior portion of the ovarian tubule has become much attenuated and unsegmented. Measurements: ovarian tubule, 6.4 mm.; terminal chamber, 1.2 mm.; uterus and vagina, 1.0 mm.

THE LIFE-HISTORY OF *SITONES LINEATUS* AS OBSERVED IN FOREIGN COUNTRIES.

It is interesting to note that Molz and Schroder⁽¹⁸⁾ consider *S. lineatus* as being double brooded in Germany, while in Denmark Rostrup⁽²⁰⁾ believes that this species has two generations in the year, the larvae of one generation overwintering, those of the other generation occurring in mid-summer. Kemner⁽²¹⁾ only refers to one generation in the year of this species in Sweden, and Baranov⁽¹⁷⁾ who gives a most interesting and detailed account of the life-history of *S. lineatus* in Russia, assumes that there is only one generation in the year, as the weevils which emerged in summer from eggs laid by the hibernated parents were not observed to pair the same summer.

NATURAL ENEMIES.

BIRDS.

Poultry eat these weevils readily. At the time of harvesting the peas and beans numbers of weevils are brought into the stackyard and many are then picked up by poultry. Miss Ormerod recorded that starlings occurred in numbers on pea fields infested by weevils.

PARASITES.

Ectoparasite. On August 4th I observed two specimens of *S. lineatus* each attacked by a mite which Mr S. Hirst has kindly examined for me. He thinks it probable that the mite—which is a larval form—belongs to the genus *Trombidium* or some closely allied genus. The mite occurred under the elytra of the beetle, lying upon the fourth to the seventh abdominal tergites, with its mouth-parts inserted in the body of the beetle between the junction of the fourth and fifth abdominal tergites. The mites were bright red in colour with pinkish legs and pale mouth-parts. One measured 0.93 mm. long by 0.49 mm. broad, the other 1.5 mm. long by 0.84 mm. broad. The weevils they were found upon had been collected from a bean field at Alness, Ross-shire, on August 2nd, and were both old males that had emerged the previous autumn. Neither seemed to be much the worse for the presence of the mite.

Endoparasites. (1) *Insectivorous.* I have bred a considerable number of the Braconid, *Perilitus rutilus* Nees from imagines of *Sitones lineatus*. I have found this parasite to occur on *S. lineatus* both in the south of England and in the north of Scotland. I am indebted to Mr G. T. Lyle for his identification of this and the following species, and to Mr K. G. Blair for passing on my inquiry to him. As I am at present engaged in the investigation of the life-history and habits of this parasite I hope to publish a complete account of it in a later paper. I have also bred a few specimens of two other species of Braconidae from imagines of *S. lineatus* collected in Suffolk by Mr B. S. Harwood. These are *Pygostolus falcatus* Nees, the fuscous variety described by Ruthe, and *Liophron muricatus* Hal, var. *nigra*. Both appear to be rarer parasites of *S. lineatus* than is *Perilitus rutilus* Nees.

(2) *Fungoid.* The most effective parasite of *S. lineatus* that I have yet observed is a fungus *Botrytis bassiana* (Balsamo) Montagne, the Muscardine of silkworms, which has been identified for me through the kindness of Mr A. D. Cotton and Mr R. Beer at the Mycological Laboratory, Kew. This fungus is particularly common upon weevils of *Sitones* kept under artificial conditions, but I have also observed specimens of *S. lineatus* attacked by it in the field. It is always fatal to the weevil attacked. While most easily observed upon the adult, I have proved experimentally that it also causes death to the pupae and to the larvae in all stages of development. Many experiments have already been carried out on infecting the weevil with spores of the fungus both in the laboratory and under muslin sleeves out of doors, all of which have

proved successful, death occurring nine to thirteen days after infection. It is therefore intended to continue this work on a larger scale and to record the results later.

In conclusion my thanks are due to Mr F. V. Theobald for encouraging me to undertake this research, and to Dr R. Stewart MacDougall for valuable help and advice in its prosecution and for the reading of this paper. I am also indebted to Mr H. Britten for identifying the weevils for me, to Miss L. H. Huie for much valuable advice in technique and other matters, to Mr P. F. Kendall for assistance in carrying out parallel breeding experiments at Wye, and to Dr W. Ritchie for valuable hints in making preparation of my dissections.

As I am at present engaged in the investigation of the life-history and habits of *Sitones puncticollis*, *flavescens*, *hispidulus*, *humeralis*, *sulcifrons*, and *crinitus*, I should be extremely grateful if any interested in the subject would forward me specimens of any of these species found injuring leguminous crops, together with full particulars.

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THE STRUCTURE, BIONOMICS, AND ECONOMIC IMPORTANCE OF *SAPERDA CARCHARIAS* LINN., "THE LARGE POPLAR LONGHORN."

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(With Plates XX-XXIII and 25 Text-figs.)

THE assurance that a definite scheme of afforestation is to be established in Britain has given a fresh stimulus to the study of insects injurious to our forest trees. Already observations on the life histories and habits of such forms have been called for, as without a knowledge of these, no definite measures of control whether preventive or remedial can be undertaken.

The following intensive research on the structure, habits and life history of *Saperda carcharias* Linn. the "Large Poplar Longhorn" is therefore opportune, for to forester and nurseryman the species is of primary importance as it may prove to be very destructive to healthy young poplars.

In the adult stage the Large Poplar Longhorn causes some injury by feeding upon the leaves and by ovipositing in the basal portions of the stems, but the greatest amount of damage is done by this insect, while in the larval state, for by the larvae feeding and boring in the stems, and occasionally tunnelling into side branches, healthy trees are very soon killed or rendered worthless.

The genus *Saperda* (Fabricus), to which our species belongs, contains about fifty species, but of these only eight are European. In Britain only three species are found, viz.: *Saperda carcharias* L., *S. scalaris* L., and *S. populnea* L. Of these only the two first named have been found in Scotland, and as far as we know, only *S. carcharias* and *S. populnea* are of economic importance, the third species being known mostly to Coleopterists and highly prized by them on account of its handsome colouration.

In England, *S. carcharias* is a fairly well known beetle, but in Scotland,

it is little known, its occurrence according to Fowler⁽¹⁾ being very rare. However, in certain areas in the neighbourhood of Aboyne, Aberdeenshire, I have found this species present in large numbers doing great damage among the young poplars of natural growth. In gardens, too, in the village of Aboyne where poplars have been planted for ornamental purposes, these have been completely destroyed through the repeated attacks of *S. carcharias*.

It was in these areas that the study of the life history of the insect was carried out by experiment and field observations, while the anatomical and microscopical studies and some breeding experiments were undertaken in Dr Stewart MacDougall's laboratory in Edinburgh University.

CHARACTERS OF THE GENUS SAPERDA.

The genus *Saperda* is singled out by Fowler⁽²⁾ from the other Lamiidae, the sub-family to which it belongs, by the following characters—

Femora not or scarcely clavate.

Thorax without lateral spines.

Tarsal claws simple.

Anterior coxae distant.

Antennae ringed with white.

Mesosternum not protuberant between intermediate coxae.

Form elongate.

Antennae eleven jointed.

In view of the work of Gaban⁽³⁾ and Felt⁽⁴⁾ this key of Fowler's, in which he places the genus *Saperda* under the forms with simple claws, requires modification.

Those two workers point out that, although simple claws are present in some species, *e.g.* *Saperda populnea*, others possess bifid claws. In the species which possess bifid or compound claws these are confined to the male sex. The bifid claws sometimes are found in the first two pairs of legs as in *Saperda carcharias*, sometimes only in the first pair of legs and sometimes only in the second pair of legs. According to Le Conte, who was the first worker to draw attention to the presence of these claws in the genus *Saperda*, it is only the inner or anterior claw of the tarsus that is toothed, or bifid.

The following is Fowler's⁽¹⁾ description of *Saperda carcharias* adult:

One of the largest and most conspicuous British Longicorns, black, clothed with yellowish or ashy-grey pubescence which is thicker and longer on the under surface

¹ The numbers in brackets refer to the "Literature," p. 342.

than on the upper, and is somewhat variable in colour, so that the insect appears to vary from quite a lighter grey to an ochreous-yellow; head large, antennae tapering with the apical joints not ringed with white; thorax slightly transverse, coarsely and rugosely punctured, with a central line and a tubercle on each side of it which are usually covered with pubescence; scutellum large, semicircular, elytra broad, with well marked shoulders, gradually narrowed at apex, which terminate at suture in a short blunt spine, very coarsely and deeply punctured, with a transverse patch of closer pubescence on each about the middle; legs short and stout, pubescent, extreme apex of femora usually black. L. 20-28 mm.

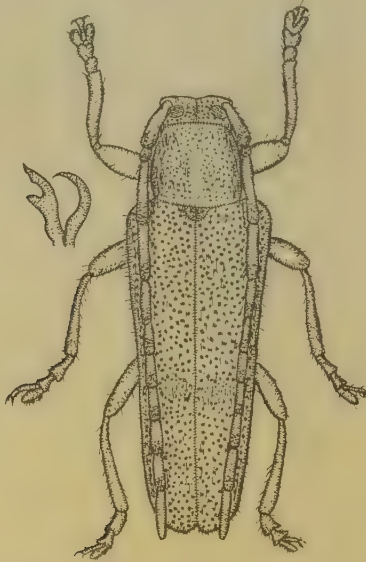


Fig. 1. The large poplar Longhorn, *Saperda carcharias* L. Male. Tarsal claws of a foreleg are shown on the left (both greatly magnified).

Male (Fig. 1) with antennae a little longer than the body, and the elytra more narrowed behind; female (Fig. 2) with the antennae a little shorter than the body, the elytra slightly narrowed behind and the fifth ventral segment of the abdomen with a fine channel towards base.

SEXUAL DIFFERENTIATION IN *S. CARCHARIAS*.

From my observations made in handling a very large number of individuals of both sexes, I find there is no difficulty in differentiating them, for not only are they different in size but they also differ in their general form; there is the difference also in the tarsal claws to which I have already referred.

A further distinguishing sex character, noticeable in the majority of my northern specimens is that of colour. The majority of the males are dark ash-grey, while all the females are greenish-yellow. Later in this work I refer to this difference in colour between the sexes.

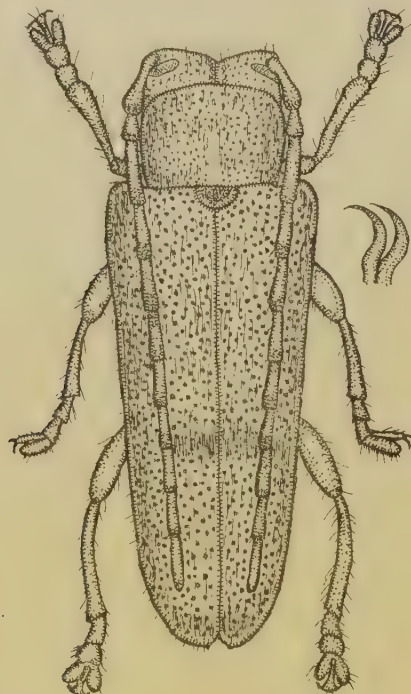


Fig. 2. The large poplar Longhorn, *S. carcharias* L. Female. Tarsal claws of a leg are shown on the right (both greatly magnified).

The principal external differences in the sexes may be thus contrasted:

	Male (see Fig. 1)	Female (see Fig. 2)
Size	18 mm.-22.5 mm.	24.5 mm.-27.5 mm.
Length of antennae ...	Longer than body	Shorter than body
Shape of prothorax ...	Quadrate	Broader than long
Tarsal claws of 1st and 2nd pairs of legs ...	One claw bifid or toothed	Simple
Breadth of elytra at base	7 mm.-7.5 mm.	8.5 mm.-9.5 mm.
Shape of elytra ...	Outer margins taper markedly towards apices	Outer margins taper less markedly towards apices
Shape of abdomen ...	Thin; groove on 5th sternite absent	Stout; groove on 5th sternite present and conspicuous

Egg of S. carcharias.

The egg when newly laid is elongate, rounded at the ends and oval in section. Its length ranges from 3.5 mm. to 4.1 mm., and it measures from 1.5 mm. to 1.8 mm. at its greatest breadth. The shell is very tough, being almost leathery in texture, has a smooth surface, and is dull yellow in colour. In general, its colour resembles very much that of the bast or outer wood in which it is deposited. It is not uncommon to find in eggs which have been laid for some time, that as a result of the pressure to which they are subjected, their shells have taken the pattern of the grain of the fibres with which they are in contact. So closely does the colour of the newly laid egg harmonise with that of the tissue in which the egg is deposited, that on several occasions in my first attempts to

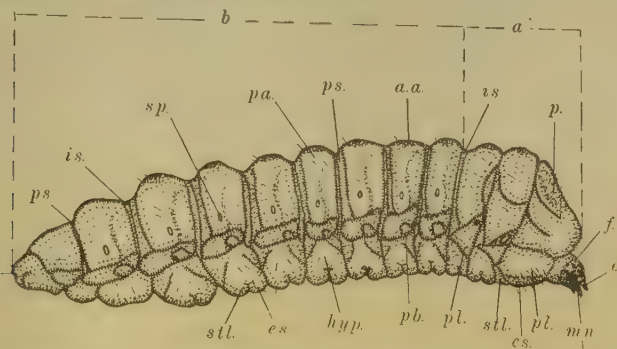


Fig. 3. Larva of *S. carcharias*, side view (greatly magnified). *a*=thorax; *aa*=ambulatory ampulla; *b*=abdomen; *es*=eusternum; *f*=frons; *hyp*=hypopleurum; *is*=inter-segmental skin; *l*=labrum; *mn*=mandible; *p*=pronotum; *pa*=parascutal area; *pb*=pleural band; *pl*=pleural lobe; *ps*=postscutellum; *sp*=spiracle; *stl*=sternellum

expose the eggs to view by carefully tearing away the outer bast layers, my eye was so deceived that the eggs were accidentally destroyed.

In the case of over-wintered eggs the colour of the shell is dark brown and the egg itself is much swollen, in fact such eggs look like small Dipterous puparia.

As compared with eggs found *in situ*, those dissected out of an egg-laying female are somewhat different in shape and different in colour; they are elongate-oval, circular in section and pure white in colour.

Larva of S. carcharias (Fig. 3).

The larva of *S. carcharias* is a typical Lamiid larva and is extremely well adapted to its mode of life. It is a soft, fleshy, legless grub, elongate

in form, and almost cylindrical in section. It varies in length from 4.5 mm. when newly hatched, to about 37.5 mm. or over when fully grown.

It is broadest across the first thoracic segment, and gradually tapers towards the tip of the abdomen. The body is deeply wrinkled and is covered with fine scattered hairs.

The larva is made up of the chitinous head-piece and thirteen segments, the first three of these forming the thorax, the remaining ten the abdomen.

The head portion is highly chitinised and posteriorly is deeply sunk in the first thoracic segment.

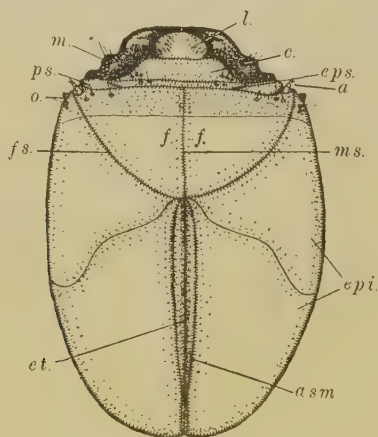


Fig. 4. Head of larva, *S. carcharias*, seen from above (greatly magnified). *a*=antenna; *asm*=attachment area of the superior retractor muscles of the head; *c*=clypeus; *epi*=epicranium; *eps*=epistome; *et*=epicranial suture; *f*=frons; *fs*=frontal suture; *l*=labrum; *m*=mandible; *ms*=median suture; *o*=ocellus; *ps*=pleurostome.

The thoracic segments are somewhat larger than the abdominal ones. The eighth and ninth abdominal segments taper posteriorly and are smaller than the others, while the last or tenth segment is made up of three lobes surrounding the anus.

There are ten pairs of spiracles, the first pair being the largest. The first pair of spiracles lie in a hollow between the first and second thoracic segments. The second pair, which are very small, are present on the third thoracic segment while the other pairs are borne by the first eight abdominal segments. Each spiracle is oval in shape and is surrounded by a chitinous ring.

The Head (Fig. 4).

If the head of the larva be dissected out from the first thoracic segment and examined under the binocular microscope, the following parts are seen: in the centre of the field is the triangular region of the frons (*f*), bounded on each side by the frontal suture (*fs*), and divided into two by the median suture (*ms*).

At the base of the triangular frons is a narrow area, the epistome (*eps*), on each side of which is a very highly chitinised area, the pleurostome (*ps*). Anterior to the epistome is the clypeus (*c*), trapezoidal in shape and

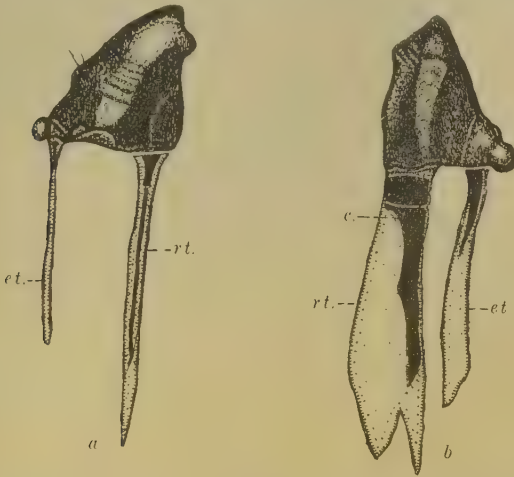


Fig. 5. Left mandible of larva, *S. carcharias* (greatly magnified). *a*=dorso-lateral view of mandible; *b*=ventral view of mandible; *c*=chitinous plate; *et*=extensor muscle; *rt*=retractor muscle.

bearing a few bristles on the sides; attached to the clypeus anteriorly is the bristly labrum (*l*) which is almost semicircular in shape.

On each side of the clypeus and labrum can be seen, in part, the mandibles (*m*). Each mandible (see Fig. 5) is strong and robust, shiny-black in colour and highly chitinised. Their general form is triangular and their inner cutting edges are produced into two blunt teeth. Each mandible is worked by two powerful muscles, an extensor (*et*) attached to the dorso-lateral surface of the mandible and a retractor (*rt*) to its inner or ventral surface. The retractor muscle is far the stronger of the two. Embedded in each muscle is a thin sheet of chitin (*c*).

Between the pleurostome (Fig. 4, *ps*) and the anterior angles of the frons (*f*), the antennae (*a*) are placed. Each antenna is sunk in a hollow and is five-jointed; alongside the small fourth joint of the antenna and external to it is the fifth joint, the smallest of all.

On each side of the frons (*f*), to the outside of the antenna (*a*) and somewhat posterior to the latter, is situated an ocellus (*o*). The ocelli have the appearance of minute knobs or nodules.

In Fig. 6 the view of the epistomal region is much enlarged and the various details will be more clearly understood by referring to it.

Looking now at the parts of the head posterior to the frontal suture (*fs*, Fig. 4), one can make out the epicranium (*epi*) divided into two by the epicranial suture (*et*), and lying in a groove (*asm*), the latter forming the attachment area of the superior retractor muscles of the head.



Fig. 6. Region of epistome, *S. carcharias* larva (very highly magnified). *a*=antenna; *c*=clypeus; *eps*=epistome; *f*=frons; *fs*=frontal suture; *l*=labrum; *o*=ocellus; *ps*=pleurostome.

From the apex or posterior angle of the frons (*f*) a curved marking may be observed to run across the epicranium. This marking forms the anterior boundary of the portion of the head sunk in the first thoracic segment.

Looking now at the head ventrally (Fig. 10, *b*) one can distinguish anteriorly the maxillae.

Examining these parts in detail (Fig. 7), on each side (the outermost parts in this view) lies the 1st maxilla, composed of five portions; the cardo (*c*); next the stipes (*st*) bearing a few chitinous bristles and with its posterior portion strengthened by a band of thicker chitin; the maxillary palpifer (*mzp*) which bears a three-jointed maxillary palp (*mp*) to the outside and the lacinia (*la*) to the inside, the latter covered with stiff bristles.

In the centre of the field lie the fused 2nd maxillae or labium. This region of the mouth parts is made up of the mentum (*m*) and the labial

palpifer (*lf*) with a few bristles; this palpifer carries the two-jointed labial palps (*lp*) and the ligula (*l*) densely covered with bristles. The submentum (*sm*) is posterior to the mentum, while surrounded by these two portions and by the cardo (*c*) and stipes (*st*) is an area somewhat circular in shape, the maxillary sclerite (*mxs*); the exact demarcation lines of this last named portion are in most cases difficult to make out.

If the mandibles and ventral mouth parts described above be removed and the under surface of the head (Fig. 8) examined, one can make out in the centre a large opening, the occipital foramen (*of*) through which may be seen the head muscles (*hm*); between this foramen and the maxillary foramen (*mf*), now clear to view, lies the region called the

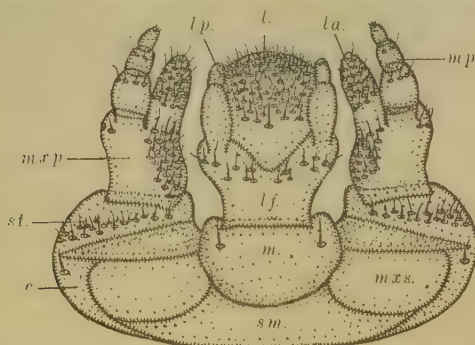


Fig. 7. Maxillae and labium of *S. carcharias* larva (greatly magnified). *c*=cardo; *l*=ligula; *la*=lacinia; *lf*=labial palpifer; *lp*=labial palp; *m*=mentum, *mp*=maxillary palp; *mxp*=maxillary palpifer; *mxs*=maxillary sclerite; *sm*=submentum; *st*=stipes.

gula (*g*); its lateral sutures diverge posteriorly and meet the tentorial region (*t*); beside the gula, on each side, lies the hypostome (*hs*) with its external suture convex.

Other portions seen in this view of the head, already referred to in describing the dorsal view, are the pleurostome (*ps*), lying on the lateral margin of the maxillary foramen (*mf*); the clypeus (*c*), the labrum (*l*), attached to which are two strands of chitin called the labral hooks (*lh*), the ocelli (*o*) and the ventral portion of the epicranium (*epi*).

The Thorax (Fig. 3, a).

In side view, immediately following the chitinous head piece we have the prothoracic, the mesothoracic and the metathoracic segments. Of these three segments the prothoracic is far the largest, being nearly equal

in size to the other two taken together. Besides differing in size, the prothoracic segment differs considerably in structure from the other two thoracic segments.

Viewed from the side the prothorax shows the following regions: dorsally the large pronotum (*p*), laterally the pleural lobe (*pl*), and ventrally the eusternum (*es*)¹ and the sternellum (*stl*). The mesothoracic and the metathoracic show, in side view, the mesonotum and metanotum respectively on their dorsal surface, the pleural lobe medially, and the eusternum (*es*) and sternellum (*stl*) ventrally (see Fig. 10, *b*). Ventral to the pleural lobe and lying between it and the eusternum and sternellum,

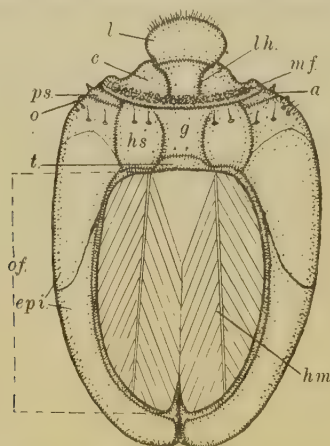


Fig. 8. Head of larva of *S. carcharias*, seen from below; the maxillae, labium, and mandibles removed (greatly magnified). *a*=antenna; *c*=clypeus; *epi*=epicranium; *g*=gular plate or gula; *hm*=muscles in head; *hs*=hypostome; *l*=labrum; *lh*=labral hooks; *mf*=maxillary foramen; *o*=ocellus; *of*=occipital foramen; *ps*=pleurostome; *t*=tentorium.

is the hypopleurum (*hyp*). Situated in a cavity between the prothorax and the mesothorax is the large thoracic spiracle, while on the metathorax lies the small spiracle.

The Abdomen (Fig. 3, b).

The first seven abdominal segments are similar in structure to each other and show the following regions: the swollen parascutal lobe (*pa*)

¹ The terminology used in this description of the larva is that adopted by F. C. Craig-head in *Report No. 107, U.S. Dept. of Agriculture*, 1915. "The Larvae of the Prioninae." See also, *A Preliminary Synopsis of Cerambycoid Larvae*, by J. L. Webb, Tech. Series, No. 20, Part V, Bureau of Entomology, U.S. Dept. of Agriculture, 1912.

and the postscutellum (*ps*) dorsally (described more fully below); the pleural zone or lobe medially; the hypopleurum (*hyp*), eusternum (*es*), and sternellum (*stl*) ventrally.

Dorsal to the pleural zone on each segment a spiracle (*sp*) is situated. On each of the pleural folds there is a swollen band (*pb*) bearing fine hairs.

The eighth body segment, in side view, has a similar appearance to the first seven, only no parascutal, hypopleural, eusternal, or sternellar lobes are present.

The ninth segment is similar to the eighth, only it lacks spiracles and shows no postscutal area.

The tenth abdominal segment is divided by three deep sutures into three lobes—one dorsal and two latero-ventral—which surround the anus.

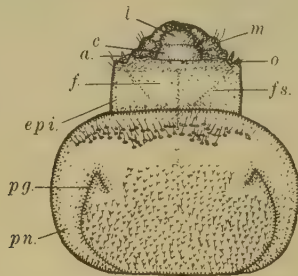


Fig. 9. Dorsal surface of first thoracic segment of larva, *S. carcharias*. Head also shown here in natural position (both parts greatly magnified). *a*=antenna; *c*=clypeus; *epi*=epicranium; *f*=frons; *fs*=frontal suture; *l*=labrum; *m*=mandible; *o*=ocellus; *pg*=pronotal groove; *pn*=pronotum.

Between the segments are bands of intersegmental skin (*is*). This allows free longitudinal expansion and contraction of the segments. This skin is more marked between some of the segments of the body than between others.

Looking now at the larva dorsally, one can see clearly the large pronotum (Fig. 10 *a*, *p*) lying immediately behind the head. In the enlarged view of this region (Fig. 9) the pronotum (*pn*) is seen to bear on each side a curved groove (*pg*), running anteriorly and then sharply bending backwards for a short distance. Between these two grooves there are numerous chitinous asperities, while running transversely along the anterior margin of the pronotum is a row of chitinous bristles. The dorsal area of the second thoracic segment—the mesonotum—shows a transverse row of very short stiff bristles along its anterior margin,

while that of the metanotum shows a double row of similar bristles with a depression between them.

The dorsal areas of the first seven abdominal segments resemble each other in appearance; they have fleshy protuberances which show two transverse depressions and bear short, stiff bristles. These bristles are arranged as in Fig. 10 *a*, and the areas which bear them are known as the ambulatory ampullae (*aa*).

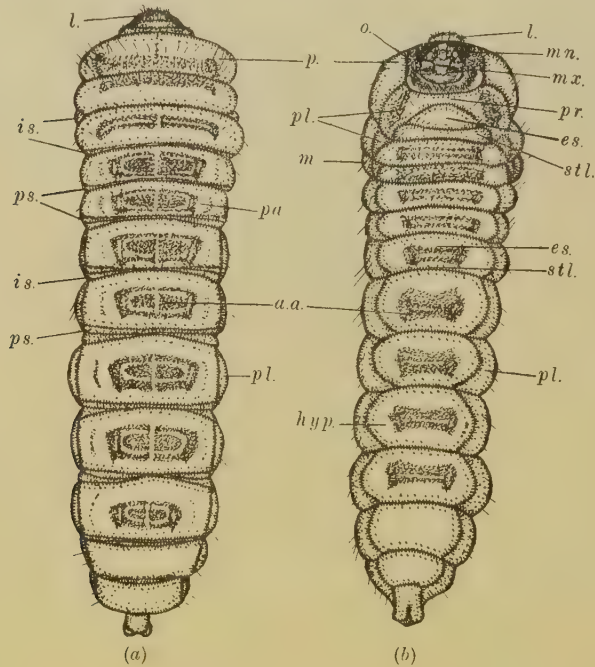


Fig. 10 *a*. Larva of *S. carcharias*, dorsal view (greatly magnified). *aa*=ambulatory ampulla; *is*=intersegmental skin; *p*=pronotum; *pa*=parascutal area; *pl*=pleural lobe; *ps*=postscutellum.

Fig. 10 *b*. Larva of *S. carcharias*, ventral view (greatly magnified). *es*=eusternum; *hyp*=hypopleurum; *l*=labrum; *m*=metanotum; *mn*=mandible; *mx*=maxillae; *o*=ocellus; *p*=pronotum; *pl*=pleural lobe; *pr*=presternum; *stl*=sternellum.

Surrounding each ampulla is an elliptical area, slightly swollen laterally, called the parascutal lobe (*pa*). Behind the ampulla on each segment is the postscutellum (*ps*). The eighth segment resembles the previous segment but has no ampulla and therefore no parascutal area. The ninth is similar to the eighth only it shows no postscutellar area. The

tenth segment has the dorsal lobe rounded in shape above, and the ventral lobes projecting in part from below it. In all the thoracic and abdominal segments except the tenth abdominal, the pleural fold or lobe (*pl*) is seen projecting on each side of the larva.

Now laying the larva on its dorsal surface so as to view it from the ventral side, the first thoracic segment (Fig. 10 *b*) shows three regions or folds, the presternum (*pr*), the eusternum (*es*), triangular in shape, and the sternellum (*stl*), almost rectangular in form.

On the mesothoracic and metathoracic segments, in ventral view, may be seen a thick row of short stiff bristles divided transversely by a depression into two folds, the anterior of which is the eusternum (*es*), and the posterior, the sternellum (*stl*).

The first seven abdominal segments resemble each other in appearance. Their sternal areas are developed into fleshy protuberances, the ambulatory ampullae (*aa*) carrying short stiff bristles (Fig. 10 *b*). The sternal ampullae however show only one transverse depression. Each ampulla is surrounded by a swollen area called the hypopleurum (*hyp*).

The eighth and ninth segments show no ampullae and hence no hypopleura; the tenth shows the two latero-ventral lobes. In all the body segments except the last the pleural lobe (*pl*) is seen projecting laterally; in the first thoracic segment this area may be easily picked out by its reddish-yellow colour.

The Pupa.

The pupa (Figs. 11–13) at first is shiny-white in colour. As development progresses, a darker colour is first noticeable in the eyes and mandibles. Later, the whole of the body takes on the colour of the adult insect. The size varies slightly in the sexes and in different specimens of the same sex. In length, the male is on an average 24 mm. while the average breadth at base of the elytra is about 7.5 mm. In the female, the average length is 26 mm. while in breadth it measures 9 mm. The head has the same general appearance as that of the adult, only it is bent underneath the body so that the mouth parts point backwards.

In a side view of the pupa (Fig. 11) the various appendages of the body are visible. The antennae (*a*) arise on the side of the head in front of the eyes (*ey*), and are directed backwards along the sides of the body, their apical portions curling round and lying alongside the first two pairs of legs. The joints of the antennae are ill-defined and hence their number cannot be made out with accuracy, but the difference in length of the antennae in the sexes is as marked as in the case of the adult insect. In

the pupa of the male, the antenna usually curls forward to the base of the femur of the first pair of legs; in the case of the female the antennae curl forward to the apices of the tibia (*d*) of the first pair of legs and lie alongside the tarsi (*t*) (Fig. 13).

Attached to the prothoracic segment (*pr*) is the first pair of legs, which are folded underneath the body (Fig. 11), and show the typical parts, coxa (*n*), femur (*f*), tibia (*d*), the tarsus (*t*).

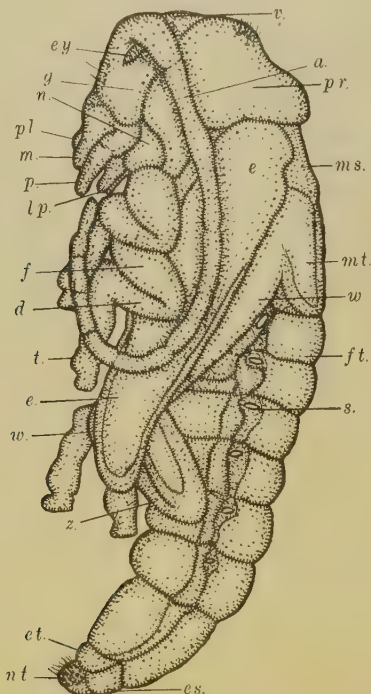


Fig. 11. Pupa of *S. carcharias*, female, side view (greatly magnified). *a*=antenna; *d*=tibia of leg; *e*=elytra; *es*=eighth tergite; *et*=eighth sternite; *ey*=eye; *f*=femur of leg; *ft*=first tergite; *g*=gena; *lp*=labial palps; *m*=mandible; *ms*=mesonotum; *mt*=metanotum; *n*=coxa; *nt*=ninth sternite; *p*=maxillary palps; *pl*=labrum; *pr*=pronotum; *s*=spiracle; *t*=tarsus; *v*=vertex of head; *w*=wing; *z*=hind leg.

The mesothoracic segment (*ms*) bears the elytra (*e*) or wing-covers. These lie between the body and the first two pairs of legs, and extend in a postero-lateral direction, their tips lying directly underneath the body. The mesothoracic segment also bears the second pair of legs. The metathoracic segment (*mt*) has attached to it the wings (*w*), which are

flattened against the under surface of the elytra (*e*). Each wing projects in part beyond the outer margin of the elytron, under which it lies. The metathoracic segment also bears the third pair of legs (*z*) which lie between the body and the elytra.

The mesothoracic segment and the first five abdominal segments carry each a pair of spiracles (*s*). The spiracles are oval in shape. The thoracic spiracle, as in the larva, is far the largest one.

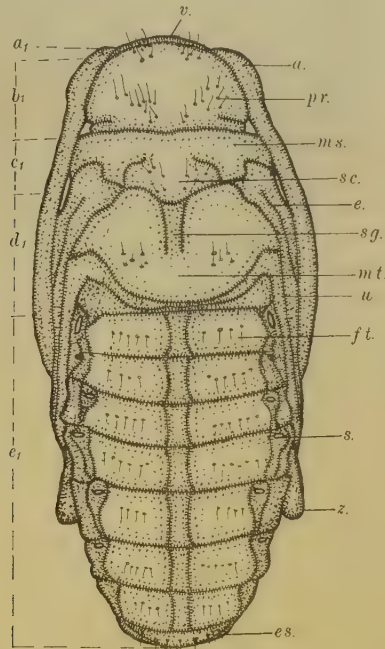


Fig. 12. Pupa of *S. carcharias*, dorsal view (greatly magnified). a_1 = head; b_1 = first thoracic segment; c_1 = second thoracic segment; d_1 = third thoracic segment; e_1 = abdomen; *sc* = scutellum; *sg* = scutellar groove; other letters as in Fig. 11.

In the dorsal view of the pupa (Fig. 12) it is seen that all the segments of the thorax and abdomen bear bristles, the prothoracic (*pr*) bristles being more marked than those of the other segments.

In the centre of the mesothoracic segment (*ms*) lies the scutellum (*sc*), while the metathoracic (*mt*) shows a fairly wide longitudinal groove, the scutellar groove (*sg*).

In the ventral view of the pupa (Fig. 13) the various parts of the head and mouth are clearly discernible. Anteriorly lies the vertex (*v*) and in the centre the frons (*fr*); on each side is the gena (*g*) or cheek region. The mandibles (*m*) are attached to the frons; between them lies the triangular labrum (*pl*). Below the mandibles are the labial palps (*lp*) in the centre, and on each side, a maxillary palp (*p*).

The ventral surface of all the abdominal segments with the exception of the last two is smooth. The penultimate or ninth abdominal segment

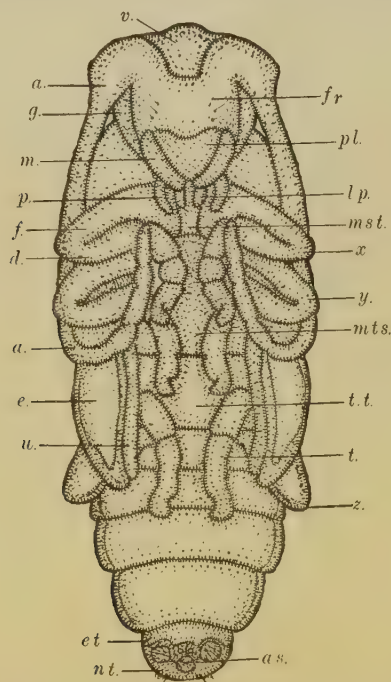


Fig. 13. Pupa of *S. carcharias*, ventral view (greatly magnified). *as*=anal or tenth segment; *fr*=frons; *mst*=mesosternum; *mts*=metasternum; *tt*=third sternite; *x*=first leg; *y*=second leg; other letters as in Fig. 11.

(*nt*) bears on its lateral margins a patch of stiff bristles. The last or anal segment is somewhat triangular in shape; it is enclosed by the eighth (*et*) and the ninth (*nt*). There is a strongly marked sexual difference between the anal segment of the male pupa and that of the female (see Fig. 14). In the male (Fig. 14 *b*) this segment shows the anal opening (*an*) with a small membranous plate (*c*) trapezoidal in shape on its anterior margin;

in the female (Fig. 14 *a*) instead of the membranous plate there are two globular tubercles (*at*) placed anteriorly side by side.

THE REPRODUCTIVE ORGANS.

Saperda carcharias has, in my observation and breeding of it, a short adult life in comparison with some Curculionid and Scolytid beetles, only about two months, and its reproductive organs, though not quite mature on the issue of the imagines from the pupal condition, ripen in a short time.

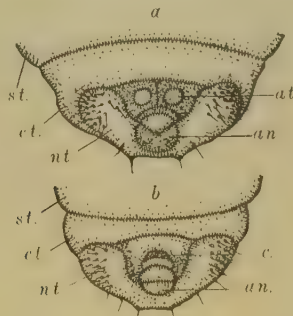


Fig. 14 *a*. Ventral view of the last three abdominal segments of female pupa of *S. carcharias* (greatly magnified). *an*=anus; *at*=anal tubercle on tenth segment; *et*=eighth sternite; *nt*=ninth sternite; *st*=seventh sternite.

Fig. 14 *b*. Ventral view of the last three abdominal segments of male pupa of *S. carcharias* (greatly magnified). *c*=membranous plate; other letters as in Fig. 14 *a*.

The male reproductive organs of Saperda carcharias.

The reproductive organs as dissected out from a male are shown in Fig. 15. They are made up of the usual parts, testes (*ts*), vasa deferentia (*vd*), seminal vesicles (*sv*), common or ejaculatory duct (*cd*), internal sac (*is*)¹ and the chitinous pieces, viz. median lobe (*ml*), tegmen (*t*), and spiculum gastrale (*sp*).

The testes (*ts*) are paired glandular bodies and lie on each side of the abdomen ventrally. Each body is dull yellow in colour and one lies

¹ In this description I have followed the terminology adopted by Sharp and Muir in their studies of the male genitalia in Coleoptera. In these studies the nomenclature of the earlier workers is reviewed and criticised *Trans. Entom. Soc. Lond.* 1912, Part III, pp. 477 *et seq.* "The comparative anatomy of the male genital tube in Coleoptera," Sharp and Muir. Also same *Journal*, 1918, Parts I and II, pp. 209-229. "Studies in Rhynchophora," D. Sharp, and "Notes on the Ontogeny and Morphology of the male genital tube in Coleoptera," F. Muir.

more anteriorly in the abdomen than the other. Viewed laterally, each body is flattened from above downwards, and is rounded at the edges. In both ventral and dorsal view each appears as a round-shaped disc with a cavity in the centre. From the centre of the cavity on the ventral

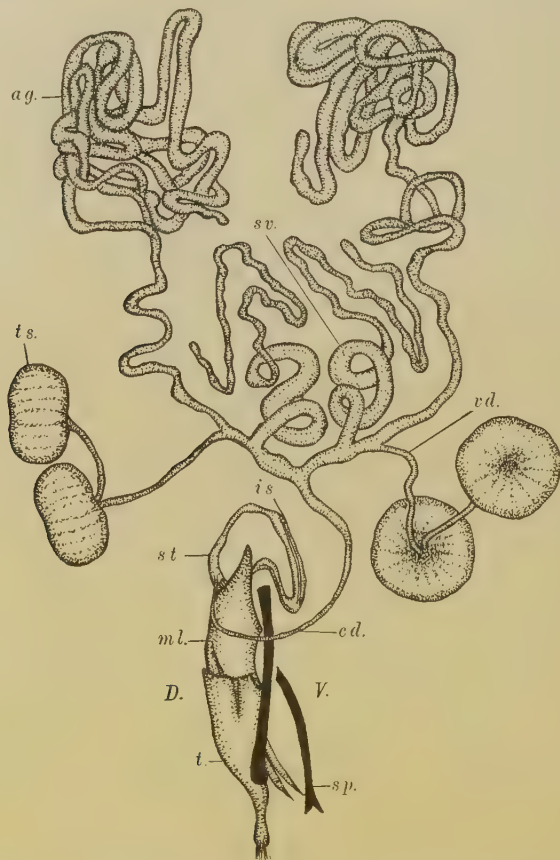


Fig. 15. Male reproductive organs of *S. carcharias* (greatly magnified). The chitinous parts are here shown in side view. *ag* = accessory gland; *cd* = common or ejaculatory duct; *D* = dorsal side of median lobe; *is* = internal sac; *ml* = median lobe; *sp* = spiculum gastrale; *st* = tube ensheathing the common duct; *sv* = seminal vesicle; *t* = tegmen; *ts* = testes; *V* = ventral side of median lobe; *vd* = vas deferens.

surface of the more anterior body, a tube arises which passes into the other body of the same testis, entering it at a point on the second corresponding to that from which it takes origin.

Just where this tube which forms the attachment between the two halves of the testis enters the more posterior body, another longer tube arises from the cavity. This tube is the vas deferens (*vd*). Each vas deferens is at first a narrow tube, which later swells out and ultimately unites with the vas deferens of the other testis, to form the common or ejaculatory duct (*cd*), leading to the internal sac (*is*) and the median lobe (*ml*).

This attachment of the glandular bodies of the testes is most interesting, as it would seem to indicate that the sperms produced in the more anterior body would have to pass through a part of the other body at least, before entering the vas deferens.

At the point where each vas deferens begins to swell out, the duct of the accessory gland (*ag*) opens into it. This gland, at its beginning, is much convoluted and ends blindly. A little further along each vas deferens, another tube, the seminal vesicle (*sv*) opens into it. This tube at its beginning is narrow; but for about a third of its length, prior to entering the vas deferens, it is much swollen and usually coils twice.

The common or ejaculatory duct (*cd*), at first a fairly wide tube, becomes more delicate and at last becomes hidden to view, ensheathed in a wide membranous tube (*st*) which is attached by muscles to the dorsal anterior surface of the median lobe (*ml*). In its course the common duct (*cd*) passes from the ventral side of the abdomen to the dorsal, and after passing through the ensheathing membranous tube (*st*), empties itself into the internal sac (*is*).

Passing into the membranous tube along with the common duct are two bundles of tracheae, which, later, enter the internal sac over the surface of which they ramify.

The internal sac into which the common duct empties itself is at first a much swollen tube, but latterly it thins out and enters the chitinous median lobe (*ml*) through the median foramen (Fig. 18 *a*, *mf*), terminating at the median orifice (*mo*) (see Figs. 16 *a* and 18 *d*).

The membranous tube (*st*) ensheathing the ejaculatory or common duct, and the internal sac, do not lead straight to the median orifice but bend several times in their course. The course of the internal sac with its various bends can be followed in Fig. 16 *a*.

At several points on the inner (external when exerted in the act of copulation) walls of the internal sac there are present chitinous structures which form the armature (see Fig. 16). On the swollen portion of the internal sac, *i.e.* between the termination of the membranous tube ensheathing the common duct and the first bend on the sac, there are

present on its ventral wall three chitinous rods (*r*). Each rod is somewhat broadened at the end of the sac next the membranous tube and is pointed at the other end.

On the ventral surface of that portion of the sac between the first and second bend, there is placed a sheet of thin chitin (*cp*), which, under the high power of the microscope, shows a radula-like surface (see Fig. 16 *b*).

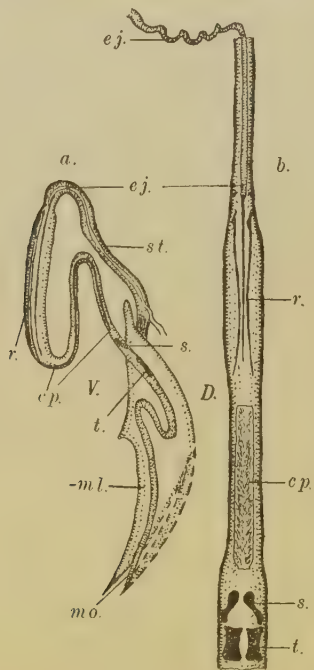


Fig. 16 *a*. Side view of internal sac and the median lobe; the latter is cut open to show course of the former; the tegmen is here removed (highly magnified).

Fig. 16 *b*. Portion of the internal sac bearing the armature is shown here straightened out (highly magnified).

cp=chitinous plate; *D*=dorsal side of median lobe; *ej*=common or ejaculatory duct; *ml*=median lobe; *mo*=median orifice; *r*=rods; *s*=first pair of chitinous rods; *st*=membranous tube; *t*=second pair of chitinous rods; *V*=ventral side of median lobe.

Just as the internal sac enters the median lobe there are present two pairs of short, stout chitinous rods.

The first pair (*s*) is placed on the lateral surfaces of the sac and arch over from the dorsal to the ventral surfaces (see Fig. 16, *s*).

The second pair of rods (*t*) lie adjacent to each other on the dorsal surface of the sac and are stouter than the first pair.

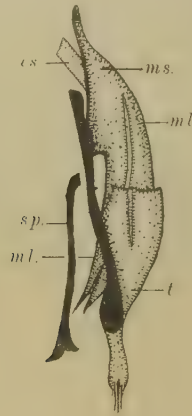


Fig. 17. The median lobe, tegmen, and spiculum gastrale, seen in side view, in their natural position (highly magnified). *is*=internal sac; *ml*=median lobe; *ms*=median strut; *sp*=spiculum gastrale; *t*=tegmen.

The median lobe (*ml*), roughly speaking, consists of a hollow curved cone of chitin pointed at its apical end. At the basal end, its dorsal surface is split into two parts called the median struts (*ms*) (Fig. 18 *a*).

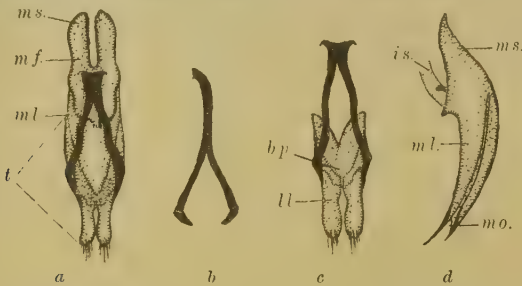


Fig. 18. The median lobe, spiculum gastrale, and tegmen showing their various parts (highly magnified).

Fig. 18 *a*. Ventral view of the median lobe within the tegmen.

Fig. 18 *b*. Ventral view of spiculum gastrale.

Fig. 18 *c*. Ventral view of tegmen.

Fig. 18 *d*. Median lobe, side view; tegmen removed.

bp=basal piece; *is*=internal sac; *ll*=lateral lobes; *mf*=median foramen; *ml*=median lobe; *mo*=median orifice; *ms*=median strut; *t*=tegmen.

For about three-quarters of its length, measured from the apical end, the median lobe is split into a dorsal and ventral portion by a membrane running along each of its sides from the median orifice (*mo*) (Fig. 18 *d*).

Ensheathing the median lobe at its pointed end is a circular ring of

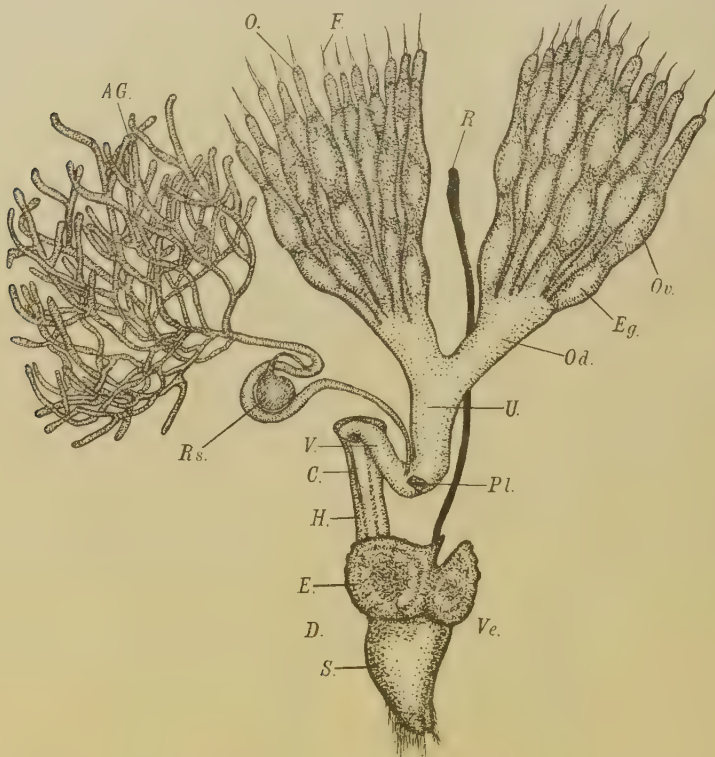


Fig. 19. Reproductive organs of female, *S. carcharias*, about to lay eggs (greatly magnified).

The chitinous portions are shown in side view. *AG*=accessory gland; *C*=support in membranous tube of ovipositor; *D*=dorsal side of ovipositor; *E*=ear of ovipositor; *Eg*=egg; *F*=terminal filament; *H*=membranous tube of ovipositor; *O*=terminal chamber of egg tube; *Od*=oviduct; *Ov*=egg tube; *Pl*=chitinous plate on uterus; *R*=stout chitinous rod of ovipositor; *Rs*=receptaculum seminis; *S*=sheath of ovipositor; *U*=uterus; *V*=vagina; *Ve*=ventral side of the ovipositor.

chitin called the tegmen (*t*). This tegmen shows a basal piece (*bp*) (Fig. 18 *c*) to which are attached two lateral lobes (*ll*). These last named portions bear on their apical parts a few stiff bristles.

Ventrally, the tegmen supports a stout chitinous arch.

The spiculum gastrale is an inverted Y-shaped piece of chitin and lies on the ventral side of the median lobe. The anterior arm of the spiculum gastrale is bent towards the dorsal surface, while the two posterior arms are somewhat hooked.

For purposes of comparison the various names of the chitinous parts of the male reproductive organs, used by Sharp and other authors, are brought together in the following table.

Lindemann (5)	Verhoeff (6)	Hopkins (7)	Nusslin (8)	Sharp and Muir (9)
Stengel	Spiculum gastrale	Fork	Spiculum gastrale	Spiculum gastrale
Gabel	Gabel	Ring	Gabel	Tegmen
Korper	Penis	Stem	Penis	Median lobe
Füsschen	Femora	Femora	Füsschen	Median struts

The Female Reproductive Organs of Saperda carcharias.

Fig. 19 shows the parts of the female reproductive organs dissected out of a beetle ready to lay her eggs.

There are two ovaries (*Ov*), one on each side of the abdomen. Each ovary consists of twelve egg tubes, each of which has a terminal chamber (*O*) with a filament (*F*) at its apex.

The eggs (*Eg*) pass from the ovaries to the oviducts (*Od*) which unite to form a common tube the uterus (*U*). Entering the posterior portion of the uterus dorsally, we have the accessory gland (*AG*) and the receptaculum seminis (*Rs*) (spermatheca).

The accessory gland, at its beginning, is composed of a series of branched tubes each of which ends blindly. Later these branches unite to form a single tube which at first is somewhat delicate.

Further along its course, the duct of the accessory gland swells out a little, finally thinning out again into a more delicate tube before it enters the uterus.

Just before the duct of the accessory gland swells out, the receptaculum seminis opens into it. The receptaculum seminis is a globular or bulb-shaped, chitinous body and lies in a bend of the duct of the accessory gland.

On each side of the uterus at its basal end is situated a chitinous plate (*Pl*). This plate, under the high power of the microscope (see Fig. 20, 1), shows a ridge (*ri*) running in a horizontal direction, dividing the plate into two halves.

Following the uterus (*U*) is the vagina (*V*), which bends forward towards the ovipositor, into which it passes.

Entering into the tubular portion of the ovipositor (see below) along with the vagina, are two bundles of tracheae ventrally, and the alimentary canal dorsally.

The ovipositor is made up of several parts—a membranous tube (*H*), a chitinous hollow sheath (*S*) and a stout chitinous rod (*R*). The membranous tube (*H*) bears several ridges on its inner surface, and enters

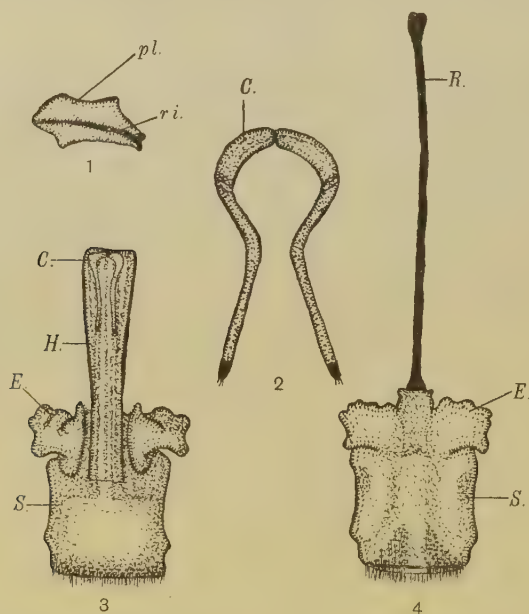


Fig. 20. Chitinous plate on uterus and the parts of the ovipositor (greatly magnified).

Fig. 20 (1). Chitinous plate at base of uterus.

Fig. 20 (2). Support in membranous tube of the ovipositor.

Fig. 20 (3). Dorsal view of membranous tube and sheath (rod portion of ovipositor removed).

Fig. 20 (4). Ventral view of ovipositor.

C = support; *E* = ear of sheath; *H* = membranous tube; *pl* = plate on uterus; *R* = rod of ovipositor; *ri* = ridge on plate of uterus; *S* = sheath of ovipositor.

the chitinous sheath (*S*) at a point about half way down the dorsal surface of the latter. The anterior end of the membranous tube is supported by a shears-shaped structure (*C*). This structure is made up of two chitinous plates (the handles of the shears) separated by a thin strip of membrane (see Fig. 20, *C*), and two membranous parts (the blades of the shears) darker coloured at their points on which are situated a few bristles.

The chitinous parts of the support lie on the inner dorsal surface of the membranous tube, while the membranous parts curve over to the ventral surface fitting into the chitinous ridges there.

The sheath portion (*S*) of the ovipositor bears on each side anteriorly an ear or wing (*E*); each wing has both a dorsal and a ventral projection. The membranous tube (*H*), already referred to, passes between the dorsal projections of the wings. These wings or ears afford suitable surfaces for the attachment of muscles, some of which play a part in the working of the ovipositor.

Borne by the anterior part of the sheath ventrally and projecting into the abdomen almost as far as the metathorax, is a stout, chitinous rod (*R*). This rod is about two and a half times the length of the sheath itself and shows grooves and ridges on its lateral surfaces. The posterior portion of the sheath is flattened dorso-ventrally and bears numerous bristles on its apical parts.

How the ovipositor is pushed out and withdrawn again I am unable to state, but three pairs of muscles which no doubt play a part in its working are worthy of note. The first pair stretches from the tip of the rod (*R*) to the anterior half of the chitinous plate (*pl*) on the uterus (*U*) (see Fig. 19). A second pair passes from the posterior half of the chitinous plate (*pl*) and attach themselves to the inner ventral surface of the sheath, while a third pair runs between the posterior half of the chitinous plate on the uterus and the ventral side of the membranous tube (*H*).

THE HABITS OF THE ADULTS.

Feeding. As soon as the adult insects issue from the stems in which they have developed, they crawl up to the leaves and proceed to feed on them.

During the daytime they do not feed to any great extent but remain motionless on the leaves; feeding takes place mostly in the evenings.

The males, after they have fed for some time, become more restless than the females and fly about from one clump of trees to another; often the males would take a bite out of a leaf here and another there, and then fly away to another tree. As far as I observed both sexes prefer the leaves of trees from three to twenty years of age.

The damage done by the beetles to the leaves is characteristic, and, in the absence of the beetles themselves, can be used as evidence that the beetles are or have been in the neighbourhood. The beetles always commence to feed on the surface of the leaf, never at the margin. Once a hole is cut through the leaf, the adult bites round and round the cut,

gradually enlarging the hole. The result is that the whole of the centre of the leaf may be completely eaten out, and only the marginal portion left intact (Fig. 21). The holes so made are of various patterns; they may be circular, oval, elongate, or irregular, but in every case the serration caused by the large biting mandibles of the adults, is distinct. By way of contrast Fig. 21 shows two different kinds of damage. In this figure the leaf on the left shows the work of an adult of *S. carcharias* in its centre, while on its edge, at the right side of the base of its stalk, is the work of a Lepidopterous larva.

Flight. Both sexes have ample powers of flight but the males being lighter than the females fly with greater ease and much more frequently.

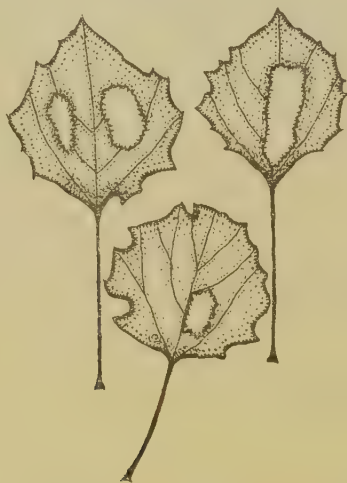


Fig. 21. Leaves of *Populus tremula* Linn. (natural size), showing characteristic injury by *S. carcharias* adult.

Taken indoors, both sexes fly readily, but in the open the females are very restful.

In the open the male beetle can soar to a considerable height. On several occasions I have noticed them as high as 30 ft. in the air. They can also fly a considerable distance at one time. The beetle in flight recalls a biplane. The outstretched elytra, held almost at right angles to the body, represent the upper plane, while the membranous wings stretched almost parallel to the elytra, correspond to the lower plane. A loud humming sound accompanies the flight of the beetle.

Stridulation. If live specimens of either sex of *Saperda carcharias* are

disturbed or touched by the hand, they emit a fairly loud uniform chirping noise which varies in intensity. This sound is produced through the rubbing of the hind margin of the pronotum upon the central anterior portion of the prolonged mesonotum. These two portions form the stridulating organs and both of their surfaces are smooth and highly polished. On the insect moving its head slowly up and down, friction is caused by the rubbing of these two polished areas upon each other, and as a result a noise is produced. The same sound can be produced in a dead beetle by imitating this action.

Pairing. The mating of the sexes takes place on the twigs and smaller branches of the trees upon which they feed. On one occasion pairing was found on a leaf. As a rule pairing occurs during the daytime and the beetles may remain in copula over night; the length of the time two beetles may remain coupled is extremely variable.

The males seemed to outnumber the females. They certainly did in the areas examined, where I estimated the proportion as 5 to 1. In my opinion the males are attracted or guided to the females through sense of smell. On one occasion I observed a male soaring in the air about fifteen yards away make a direct flight towards a female, already attended by two males, and alight beside her.

Oviposition. The female deposits her eggs in the stems of vigorously growing, healthy trees, and near the base. Prior to egg-laying, a preliminary examination is made by the female of this portion of the stem. During this survey she rubs the apex of her abdomen on the bark of the stem, at the same time swaying her body from side to side. After testing in this manner for a short time she crawls round and round the stem often returning in the opposite way. Finally when satisfied, she chooses a spot on the surface of the stem where the bark is smooth, and standing with her body at right angles to the long axis of the stem, her antennae directed backwards along the sides of her body, she gnaws a notch with her mandibles. The incision lies typically in the vertical direction, but sometimes is tilted slightly (Fig. 22). The cut measures on an average about 4.75 mm. in length. The depth of the cut varies, but on an average is about 2.25 mm. On very young stems, where the bast layers are thin, the incision usually reaches the sapwood; on older stems, *e.g.* from twelve years old and upwards, where the bast is thicker, only the outer layers of the bast are cut.

The time taken for completing the egg cavity is about ten minutes or longer, and then the female turns round and backs into the excavation, locating it with the tip of her abdomen. Next taking a firm hold of the

bark, resting mainly on her middle and hind pairs of legs, she thrusts out her ovipositor, inserts it into the incision and forces an egg through it. Before the ovipositor is withdrawn, a colourless gummy fluid is passed into the egg-incision. During this operation much muscular effort is expended, for the egg is pushed away from the egg-bite. Where the bast layer is thin, *e.g.* on stems between five and twelve years old, the egg is found firmly placed between the cambium layer and the sapwood, and about 2.5 mm. from the egg-bite. On the other hand, if the stem be



Fig. 22. Lower nine inches of 6-7 year old poplar stems showing egg-incisions and burrowings of young larvae (dark patches in figure). Two eggs and the young larval burrowings are here exposed by the tearing away of the bast and cambium layers.

older and the bast layers thicker, the egg is placed between the tissues of the bast.

The spot selected by the female for egg-laying is always a smooth portion of the stem. On no occasion have I found her laying eggs in cracks or lenticels. I am inclined to believe that the statement in continental works that eggs are laid in cracks, is due to the fact that the actual egg-laying of the beetles has not been observed, the eggs having only been noticed when the egg-incisions had begun to gape, viz. in

about one month's time from the date of laying. These cracks have been suggested as places chosen for egg-laying, the real fact being that the crack is the result of the egg-laying.

One egg only is inserted into each incision. It is quite a common occurrence, however, to find on badly infested stems, two or more eggs placed close to one another, but careful examination shows that each egg has been forced into a separate incision.

On several occasions one found females inserting their ovipositors into egg-bites without eggs being laid. It is a common occurrence to find more egg-bites on stems than there are eggs.

Owing to the position taken up by the female during oviposition, namely, with her body at right angles to the long axis of the stem, the eggs are always placed with their long axis in the horizontal direction (Fig. 22); exceptionally eggs were found slightly tilted.

The time taken for the egg-laying process is variable. In one case I observed that a female remained in the egg-laying position for five and a half minutes, while on another occasion she remained thirty-two and a half minutes.

The egg-bites, when newly cut, and into which eggs have been inserted are very narrow, to the eye appearing as a thin line, and until one gets familiar with their appearance they are very apt to be overlooked. In course of time the bites open or gape, and ultimately show as longitudinal dark cracks. In this stage they are very readily detected on the surface of stems. These bites are the only external evidence of the presence of eggs.

The total number of eggs laid by a single female is variable. The lowest number I ever counted was twenty-eight while the highest was fifty-one. All the eggs are not laid on one stem, but spread over several. As a rule the younger the stem chosen the fewer the eggs laid on it. As an illustration, I have counted as many as ten to twelve eggs on several twelve year old stems, while seven was the average number on the five year old ones.

As will have been noticed in the study of the structure of the reproductive organs of an egg-laying female, all the eggs present in the ovaries are not mature at one time, a fact further borne out in the breeding experiments described later. Usually one finds on the dissection of the ovaries of a ripe female that only twenty-four eggs are mature at one time. The time taken to complete egg-laying is variable. In my experiments it extended from fourteen days to three weeks. In one particular case of egg-laying kept under close observation, as many as eight eggs

were laid in a single day, and the female, after she had laid these, resumed feeding, and then returned to the base of the stem to complete her egg-laying. Sometimes egg-laying females were noticed to cut vertical notches much resembling egg-incisions, and so nourish themselves.

COLOURATION IN THE SEXES.

From a careful examination of a very large number of specimens of *Saperda carcharias* in the Aboyne areas, I have come to the conclusion that there are two colour varieties in the male. The majority of the males are covered with an ashy or white-grey pubescence, but others show a pubescence of a colour similar to the female, namely, greenish-yellow.

While the variety with ash-grey pubescence is the predominating variety in the Aboyne district, in other areas this variety is not nearly so plentiful.

In the Waterhouse Collection in the Entomological Department of the University of Edinburgh, none of the male specimens of *S. carcharias* show this ash-grey or white-grey pubescence.

Through the courtesy of Dr Gahan an examination was made of the collection of *S. carcharias* in the British Museum (Natural History Museum, South Kensington), but in only one example in the British collection was there any approach to the ash-grey variety, all the other specimens showed the greenish-yellow pubescence. Among the *S. carcharias* specimens from Central Europe, however, there were several males with ash-grey pubescence.

Professor Hudson Beare informs me that E. Reitter in his *Fauna Germanica*, vol. XIV. p. 64 refers to this ash-grey pubescence (ab. grisescens, Mulsant). Reitter states that specimens of this colour occur but rarely in Germany. Evidently the describer, Mulsant, makes no reference to or had not noticed this colour to be peculiar to the males. Professor Hudson Beare, in collecting specimens of *S. carcharias*, in England, has not yet met with males showing this ashy-grey pubescence.

On account of their colouration, while feeding on the leaves of their host plants, the males showing the greenish-yellow pubescence similar to the females, and the females themselves are rendered very inconspicuous (Plate XX, Right). Even while at rest on the twigs during pairing their mottled greenish-yellow colouring is to some extent effective as a means of concealing them.

In the case of the males of the ash-grey variety their concealing colouration is not conspicuous while feeding on the leaves of their host

trees, but their colour accords exceedingly well with the ash-grey bark of the twigs and branches (Plate XX, Left). During oviposition the female is not a conspicuous object, as the basal portions of the stems chosen for egg-laying are in many cases either covered with moss, the colour of which blends well with the colour of the female, or she is entirely obscured to view by ground vegetation surrounding the stems. So effective is concealing colouration in this species, that until the eye gets accustomed by search, it is very easy to pass the beetles over; on one occasion an insect which was passed unnoticed, revealed itself by the stridulation which followed a jarring of the twig, on the leaves of which the insect was resting.

THE LARVAL GALLERIES.

Of the numerous completed larval galleries examined by me on stems not badly infested and where the larvae had room to work, one form of gallery was met with far more frequently than any of the others. This form may be taken as the typical gallery (see Fig. 23).

For the sake of description the typical form of gallery may be divided into four different portions, viz. (a) the initial or horizontal portion, (b) the vertical portion, (c) the exit portion, and (d) the pupal portion.

(a) *The initial or horizontal portion.*

Upon issuing from the egg, the larva feeds at first upon the egg shell and then proceeds to destroy the tissue immediately surrounding it, viz. the inner bast layers and the cambium. In this way a minute shallow roundish patch is formed. Later the larva works its way out of the egg cavity or patch and cuts into the sapwood in a horizontal direction. As it bores, some of the gnawed material is passed through its alimentary canal, but far more is passed backwards into the gallery. As a rule the sides of this horizontal portion of the gallery are very irregular in outline and are deeply indented. The shape too of this portion is constantly being altered, as the young larva returns along it, repeatedly widening and deepening it, at the same time clearing away the frass or gnawed material, so as to keep a free air-passage to the exterior through the now gaping egg-bite.

There is great variation in the length of this portion of the larval gallery. In some cases it was fully one inch in length, while in others it was only about half that length.

(b) *The vertical portion.*

When the initial portion is completed the larva turns downwards, that is to say, at right angles to the first portion. As the larva tunnels

downwards, it gnaws gradually deeper and deeper into the sapwood until finally the centre of the stem is reached. On the root portion of the tree being reached the larva turns about and tunnels up the centre of the stem. This part, at the turning point, is much widened and is irregular in outline.

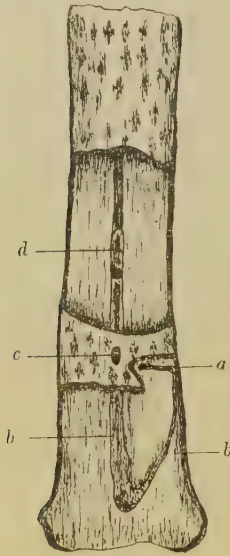


Fig. 23.

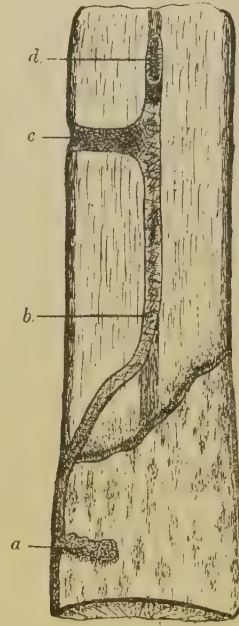


Fig. 24.

Fig. 23. Typical form of larval gallery on a 7 year old poplar stem. (The horizontal scale to which figure is drawn is much greater than the vertical.) *a*=horizontal or initial portion of gallery on outer layers of sapwood; *b*=vertical portion of gallery in wood; *c*=exit hole; *d*=pupal portion.

Fig. 24. Another form of larval gallery. Larva here after having tunnelled for some distance downwards proceeded and tunnelled upwards. *a*=horizontal portion of gallery on outer layer of sapwood; *b*=portion of gallery in wood; *c*=exit portion of gallery; *d*=pupal chamber.

(c) *The radial or exit portion.*

On its way up the centre of the stem the larva turns round and bores in the transverse direction, cutting through the sapwood and bast, and ultimately reaching the outside of the stem (see also Fig. 25). This portion of the gallery is regular in outline and is elliptical in section; its greatest breadth being in the vertical direction. In some cases, however, the exit

hole appears only as a longitudinal crack on the surface of the bark. Usually the exit hole occurs about four to six inches above the level of the ground but in a few cases it was cut well up the stem, occurring as high as one and a half feet. As a rule this portion of the gallery is not completed all at once, but the larva returns again and again from the centre of the stem until it is completed. On the completion of this portion of the gallery the larva plugs it tightly with gnawed material.

(d) *The pupal portion.*

The larva now continues to bore up the centre of the stem in the vertical direction and may reach a height of 1 ft. 9 in. or 2 ft. in the centre of the stem. By this time it is full grown and is ready for pupation. Enlarging slightly the diameter of the portion of the tunnel just cut,

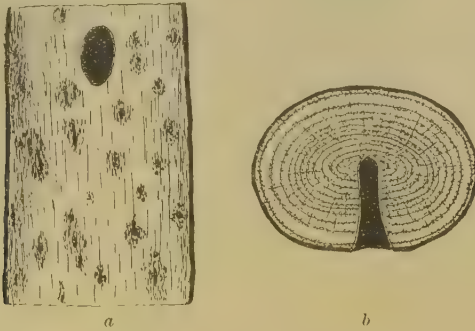


Fig. 25 a. Portion of stem of a 12 year old poplar showing oval exit hole made by larva for exit of adult.

Fig. 25 b. The same in transverse section to show the complete exit portion of gallery.

i.e. the uppermost portion, it seals the burrow tightly behind it with a dense plug of coarse frass ripped roughly from the side of the gallery. This operation being completed, the larva now within its pupal bed, ceases to feed, reverses its position, its head-end resting on the plug of frass at the lower end of the cell, shrinks slightly, moults, and the pupa is revealed. The moulted chitinous head parts of the larva are found lying in the upper end of the pupal chamber. The length of the pupal chamber is on an average $1\frac{1}{2}$ inches.

The time taken by the larva for the completion of the whole gallery, excluding the hibernating period, is about eight and a half months.

After the period of pupation has passed, the young imago bores through the plug of frass at the base of the pupal chamber, and then

gradually works its way down the centre of the stem to the exit portion of the gallery. Clearing away the frass of the exit portion, and at the same time widening and rounding off its outline, the adult finally reaches the outside and issues through the now circular exit or flight hole.

If such a gallery as that described be made on a very young stem, say a stem about five years old, one finds that the whole of the wood in the centre of that portion of the stem between the exit portion and the pupal chamber has been cut out, and only a thin outer shell remains.

Another form of gallery is that shown in Fig. 24; a modification of the form just described; it may be found in older stems. Here the larva, after tunnelling the horizontal portion of the gallery, turns at first downwards for a short distance and then returns and tunnels upwards, gnawing deeper and deeper into the sapwood, until the centre of the stem is reached. Before pupating, the larva cuts the exit portion at the upper end of the gallery, pupating as in the case of the typical form.

Irregular Larval Galleries (Plates XXI and XXII).

Where many larvae are at work together on a stem, their galleries may be very irregular both in shape and in direction. In fact, in many cases it is extremely difficult, and may be impossible, to trace an individual gallery at all. As some of the less irregular forms are merely modifications of the typical gallery, I propose to describe the parts of them in so far as they differ from the forms already described.

A specially common case is where the centre of the stem has already been tunnelled by an older larva. Here, the younger larva cuts the vertical portion of the gallery in the wood alongside the gallery already cut in the centre of the stem. In other respects the gallery cut vertically upwards by the younger larva resembles that of the typical form of gallery, only it is much shorter. Whereas the typical form of gallery cut in the pith may reach a length of almost 2 ft., it may only reach 9 inches in the irregular form. The outline too of the gallery when cut in the wood is different from that when cut in the pith. In the case of the former it is oval, elliptical or irregular in section, whereas in the latter it is almost circular.

In other cases occurring under similar circumstances to the last, but where old flight holes are already present on the stems, and within easy reach of the younger larvae, no exit hole is cut, the future imagines issuing through old flight holes. On young stems of about five years of

age it was a common occurrence to find the horizontal portions of the larval galleries running into each other, with the result that the stems were completely ringed. After the larvae had completed this portion of their galleries, they would turn downwards in the stem, completing their tunnels in one of the ways already described.

As a general rule, on very badly infested stems and where these had already been badly holed by larval tunnels, the younger larvae would tunnel in any direction where the wood was intact and make no provision for the exit of the imagines, leaving these to escape through old flight holes.

In exceptional cases, on badly tunnelled stems, the adults cut their own flight holes, choosing a part of the stem where the outer bark was fissured or where it was thin.

The Habits of the Larva in the Stem.

The manner in which the larva propels itself in the stem during feeding and the cutting of the gallery is very interesting, as apparently it can ascend or descend with equal facility. The grubs are legless, but locomotion is secured through the use of well developed dorsal and ventral ambulatory ampullae, which come into play either from the anterior or posterior end of the body in peristaltic succession. These ampullae, together with the chitinous asperities on the dorsal surface of the prothorax, braced against the sides of the gallery, constitute an efficient and rapid means of locomotion. In descending the stem the various movements may be reversed, but most commonly the larva descends head in front.

During the gnawing process the head and thorax are moved with a sidewise motion, and in this way the wood is bitten off. Some of this gnawed material is passed through the alimentary canal, but by far the most of the material is passed behind into the gallery, and is either pushed to the outside of the stem through an egg-incision or exit hole, or is pressed tightly to the sides of parts of the gallery.

The young larvae when present in large numbers in a stem develop a cannibalistic habit, and often one finds on tracing the galleries in such stems, that some of them end very abruptly. If, experimentally, a few larvae of different sizes be placed together in a box for a short time, say for an hour, the smaller ones on being examined at the end of this period will be found to have been badly bitten by the larger ones, and they subsequently die.

THE LENGTH OF THE LIFE CYCLE.

My first observations on *S. carcharias* in the open, began in Aberdeenshire, in 1915, but it was not till the following year that any definite experiments were begun with a view to the determination of the length of the life cycle.

On July 10th, 1916, in the areas where the poplars were infested with this species, I noticed on examination of a number of stems of various ages that quite a large number of young larvae were present underneath the outer bark layers. These larvae had not been long hatched, for they had just cut the tissue close to where the eggs had been deposited and had just begun to cut the horizontal portion of their galleries. To facilitate observation of these larvae later on, small notches were cut. Throughout the summer and autumn these marked stems were examined with a view to following the making of the larval burrows. Till September 28th, 1916, the larvae continued to burrow in the stems, but about this time they ceased feeding. In all the cases examined at this time the larvae had completed the horizontal portion of their galleries, and had also tunnelled the portion of their gallery in the vertical direction downwards, reaching almost the roots of the trees. In all cases the larvae hibernated head downwards. Their average length at this stage was 18 mm.

In the end of March, 1917, six of these marked plants were carefully removed from their natural habitat and replanted in an area where they could be kept under closer observation and at the same time be protected from further infestation. These young trees chosen for replanting were from five to seven years of age as at these ages they could be transplanted without undue risk to their life. Along with these marked stems four uninfested plants of a similar age were removed from the wood and replanted alongside the infested ones. Throughout the winter and early spring months, October, 1916, to March, 1917, the larvae hibernated. Examination of the stems on April 22nd, 1917, showed that the larvae were still hibernating. From April 25th, 1917, to May 5th, 1917, they showed signs of movement within their burrows, but did not recommence to tunnel and extend their galleries till about May 8th, 1917. Throughout the summer and autumn of 1917, the larvae continued to tunnel in their burrows. On October 2nd, 1917, they ceased to feed. At this date some of the larvae had attained their full growth and had completed their pupal chambers.

From October, 1917, to December, 1917, the stems containing the

full-grown larvae were examined at intervals, but no signs of pupation were shown. From January, 1918, to April, 1918, they were not examined, as during this period I was engaged in Forest Survey work for the Board of Trade Timber Supply Department. On May 16th, 1918, I re-examined these stems but still there were no signs of pupation. On May 22nd, 1918, the first larva pupated; others continued to pupate up to June 4th, 1918.

The larval period then from July 10th, 1916, to May 22nd, 1918, was about 23 months. When emergence of the adults was near at hand, the stems were screened with slips made from draper's cotton so that the adults when they emerged from the stems would not escape into the open; the adults were secured. The adult stage was reached by one female on July 2nd, 1918, but she did not emerge through the exit hole till July 14th, 1918. That is to say, the pupal stage from May 22nd, 1918, to July 2nd, 1918, lasted about forty days. Many adults, the majority of them males, issued from the stems up to July 31st, 1918. As these adults came away from the stems and collected in the cotton slips they were caught and placed in fresh cotton cages. Each cage consisted simply of a slip of cotton drawn over each of the four uninfested transplanted stems already referred to. As the foliage of the trees could not be enclosed conveniently within the cotton cage, each slip at its upper end was tied closely round the stem, while the lower end of the slip next the ground was weighted down with stones and soil. In this way a complete cage was formed and the beetles could not escape. In each cage a wide-necked bottle of water was enclosed, containing young twigs bearing leaves of the Trembling Poplar (*Populus tremula* Linn.), so that the beetles could feed on the leaves if they chose. Fresh twigs were placed in the bottles in the cages every second day. Immediately the beetles were placed in the cages they made for the leaves on the twigs and greedily devoured them.

The first pair of beetles was placed in a cage on July 16th, 1918, and a constant watch was kept for pairing, but copulation did not take place till July 26th, 1918, the beetles having fed for eleven days. As soon as pairing was observed, the pairs were marked by simply breaking off the tip of an elytron, so that they could be readily recognised. Three days after having paired, the first male beetle died. Oviposition of the first female was noticed to take place at the base of the stem enclosed in the cage, on August 2nd, 1918, and egg-laying was completed by August 15th, 1918. As soon as egg-laying was completed the female no longer fed on the fresh leaves supplied, but clung to the sides of the

cotton cage. This female lived until August 28th, 1918. In other cages similar observations were made, only the beetles lived somewhat longer. In some cases the females lived for three weeks after egg-laying was completed, while the males lived for one week after pairing.

During the period of egg-laying freshly cut pieces of stems of poplar were placed in all the cages so that plenty stem-surface would be given for the females to lay on. The eggs laid on the stems enclosed in the cages were examined at intervals to ascertain if any of them had hatched, but in no cases, even in those eggs laid as early as August 2nd, 1918, had larvae issued. Dissection of some of the eggs at the end of September, 1918, yielded young larvae.

Throughout the hibernating period, October, 1918, to May, 1919, the eggs on the stems were examined at intervals but always without any hatching. On examination of the stems on June 14th, 1919, however, some of the eggs present on the stems had hatched. Others hatched in the following days and by June 20th, 1919, all the eggs present on the stems under my notice had hatched. The egg stage in these experimental cases thus lasted about ten and a half months.

On the stems marked in July, 1916, left in the open under natural conditions, similar results were obtained as regards the length of both the larval and the pupal periods. Adults were found to escape from stems in the open—marked and unmarked—from July 16th onwards, and egg-laying was found to take place on the basal portions of the stems from August 4th, 1918, to August 25th, 1918. The principal period of emergence of the beetles was from mid July to mid August. During the period of oviposition in the open, a search of the infested areas was made for females that were laying eggs and also for fresh egg-bites. Where these were found, nicks were cut so that the places could be detected later. From August 4th, 1918, to August 25th, 1918, a large number of those egg-notches were marked. The marked stems were examined every three days throughout the late summer and autumn, but in only two cases were eggs found to have hatched. The date on which these were found was August 26th, so that the incubation period was in this case about three weeks. In all the other cases examined the eggs remained unhatched. Portions of these stems cut down in May, 1919, were kept in the open and examined at intervals, but not till June 15th, 1919, did any of the eggs on them hatch. The two cases where eggs hatched in late August, 1918, were exceptional and large numbers of stems containing eggs were examined.

During the summer of 1919 many egg-incisions were made by females

between August 3rd, 1919, and August 12th, 1919, but up till now, December 11th, 1919, none of the eggs have hatched.

From experiments and from my observations made on eggs and larvae in their natural habitat, the length of the life cycle of *S. carcharias*, in Scotland, is about four years, a very considerable part of this time being passed in the over-wintering egg-stage. In warmer conditions than in Scotland, the period of the life cycle is shorter; for example, continental writers state that in Central Europe the typical length of the life cycle is three years.

As an illustration of the influence of temperature on the length of the life cycle, I may say, that from some pieces of stem cut down in the open on January 25th, 1919, containing fully-grown larvae ready to pupate, and kept under laboratory conditions, adults emerged during the first days of May, 1919, while in corresponding material left in the open, the larvae only reached the pupal stage on May 23rd, 1919, the adult stage on July 8th, 1919, and emergence followed on July 20th, 1919.

HOST TREES.

In the areas in Aberdeenshire, where my observations were made, *S. carcharias* is attacking one species of poplar, namely, *Populus tremula* Linn.

Adults, kept in the laboratory and offered the leaves of various species of poplar fed willingly on all of them. Further, in summer, 1919, females in captivity readily laid their eggs on pieces of stem of the Black Italian Poplar (*P. monilifera* Ait.).

In the following list, the poplar species attacked by *S. carcharias* are collated from the works of the continental authorities named below. Ratzeburg⁽¹⁰⁾ records *S. carcharias* on Black Poplar; Altum⁽¹¹⁾ states that it attacks Canadian, Black and Trembling Poplars, and also willows; Schiodte⁽¹²⁾ says that the larvae are found on *Populus monilifera*, *P. ontariensis*, *P. tremula* and on willows. Kaltenbach⁽¹³⁾ names as host trees, *P. nigra*, *P. dilatata* and *P. tremula*; Tachenberg⁽¹⁴⁾ names Black Poplar, Trembling Poplar, Italian and German Poplars, also willows. Judeich and Nitsche⁽¹⁵⁾ state that the species is found on all poplars but most commonly on the aspen (*P. tremula* Linn.); Nusslin⁽¹⁶⁾ confirms this statement and adds willows as host trees. A more recent record is a Spanish one, *S. carcharias* having been found on *P. nigra* in the province of Gerona⁽¹⁷⁾.

ECONOMIC IMPORTANCE OF *S. CARCHARIAS*.

In the areas examined by myself, only vigorously growing healthy, trees between the ages of five and twenty years have been chosen for attack by *S. carcharias*; the species is therefore of considerable economic importance in our forestry. This importance lies not so much in the fact that the insect is attacking a species of poplar, namely, *Populus tremula* Linn., which is chiefly an ornamental one, but in the fact that in the absence of this host, or on a sudden increase of its numbers, as in the case of many other injurious insects, other valuable timber-producing poplar species would be endangered.

The destructive work of *S. carcharias*, both in the adult and larval stages, is partly of a physiological and partly technical nature. The adults, through their habit of eating out portions of the centre of the leaves reduce the leaf-surface of the tree, and in cases where the midribs of the leaves have been cut, the food supply is interrupted (see Fig. 21). Then there is a second kind of damage done by the adult, namely, the cutting of the egg-incisions on the basal portions of the stems (see Fig. 22). This is the more serious kind of adult damage, for, as a result of this gnawing of the egg-bites, the outer bark or bast layers and cambium may be cut. The insertion of eggs through these bites adds further to the injury of these layers. Later these incisions are the origin of the large deep fissures on the surface of infested stems. Further, the female beetles have the habit of cutting a large number of nicks on the basal portions of stems, of a similar appearance to egg-bites, but no eggs are inserted into them. Such incisions afford suitable openings or wounds for the entrance of spores of parasitic fungi. In any case should the cambium layer be destroyed in the cutting of these incisions, and this is very frequently the case in stems of small diameter, the injury gives rise to defects in the growth of the stem.

By far the greatest damage, however, is done by the larva. First of all, the larvae on hatching tunnel along the surface of the sapwood in a horizontal direction and as a result the inner bast layers, cambium and outer sapwood may be badly injured. Where there are several larvae at work, the stem can be completely girdled by the union of these horizontal tunnels and the flow of sap interrupted. On young stems, say, about five to seven years of age, the presence of only a few larval tunnels on a stem is sufficient to prevent the flow of sap. In several cases that came under my notice, the union of the horizontal portions of only two larval galleries completely ringed the stems.

Then there is the additional injury of a technical nature done by the larvae, namely, that caused through their tunnelling in the longitudinal direction in the wood of the stem (Plates XXI and XXII).

In cases where stems are badly infested with larvae, the whole of the wood may be completely riddled with such tunnels. As a result the commercial value of the wood is rendered worthless. These injuries to the wood by the larval burrowings do not alone directly cause the death of the tree. The death is due principally to injuries of the bast and cambium layers.

Further, the making of exit holes by the larvae in preparation for the issue of the imagoes, the widening of them by the imagoes, and consequently, the allowance of air and moisture into the centre of the stems, hasten still more the destruction of the wood. In many cases in which the stems had survived an earlier attack, the flight holes had been completely occluded through the growth of the outer bark layers and were completely hidden to view. Where all the wood is practically destroyed, or the stem sufficiently injured by the larval tunnels the tree is greatly weakened against wind. Hence it is not an uncommon occurrence on the examination of an infested area after a wind storm, to find many of the badly infested stems broken over at their bases.

In the areas under observation the damage done to the natural growth was very great, practically every tree from five to twenty-five years of age showed signs of infection in one stage or another. Some of the trees which had survived a bad infestation were still alive but showed a stunted growth, their bases being much swollen and bearing deep black fissures. Others had quite hollow stems, the wood in their centre having been completely destroyed (Plate XXIII).

It is evident then, that if artificial plantations or nurseries containing poplars were in the neighbourhood of areas where the natural growth was badly infested, the trees present in them would be greatly endangered and considerable loss would ensue from an attack.

EVIDENCES OF ATTACK.

The first indication that adults are present in any area of poplars may be known by examination of the leaves and stems of the trees. Should adults be present, holes on the leaves—the boundary of the wound showing serrations—will be found. This evidence of the presence of beetles is easily recognised once attention has been drawn to it, and I make special mention of this as at this stage the beetles could be looked for and collected before egg-laying had commenced or been completed.

As the principal emergence period of the beetles in Scotland, is from mid July to mid August, beetles should be looked for between these dates and collected.

To ascertain if the beetles have begun egg-laying, one has only to examine very carefully the surface of that portion of the stems between the level of the ground and nine inches upwards. As the reader will have noticed in an earlier paragraph, if egg-laying has begun, egg-bites will be found on these basal portions of the stems. These will have the appearance of short, thin, narrow markings, measuring about 4.75 mm. in length. To the left or right of each of these markings, lying either in the bast layers if these be thick, or between the cambium layer and the sapwood where the bast layers are thin, a single egg may be found.

At a later date, *i.e.* in about one month's time these bites develop into deep black cracks or scars, which, in course of time, become greatly lengthened.

As soon as larvae begin to groove the surface of the sapwood, their presence is indicated by the protrusion of coarse shreds of gnawed wood, which are thrust out through the egg-incisions. In the first year of larval life, the presence of larvae in infested stems is not well marked. It is while tunnelling the vertical portions of their galleries, that external symptoms of larval attack become very apparent. The presence of the larvae is then plainly indicated by large quantities of sawdust and wood chips, lying in heaps at the bases of the stems, having been pushed out by the larvae either through the exit hole or through cracks on the stem.

Then there is the presence of the exit holes which occur from the base to well up the stem. Should these holes be found on examination to be packed tightly with frass and to be oval in section, then the adults have not yet issued through them. On the other hand, if these holes be circular in shape and empty, then adults have escaped from the stem. In older stems which had survived earlier attacks, it was common to find the flight holes greatly enlarged, and appearing as longitudinal fissures on the surface of the stems (Plate XXIII).

CONTROL MEASURES.

With a knowledge of the life history and habits of the species, it is now possible to make definite recommendations and suggestions for its control should it ever become necessary.

Trees grown both in natural regeneration and in artificial plantations, if already infested, should be cut down and burned, as they will be a source of danger to healthier trees. This operation should be carried

out before the end of June of each year, so as to be completed before the beetles begin to emerge.

As soon as the presence of adults is indicated by the cutting of the leaves of the host plants, steps should at once be taken to seek out and collect as many of them as possible. These should be looked for, in Scotland, between mid July and the end of August.

If carried out, these two measures will ensure the destruction of a large percentage of the surviving larvae and beetles each year, so that the damage will be reduced to a minimum.

In the case of a few trees, *e.g.* park trees, oviposition may be largely prevented by ensheathing the lowermost portion of their stems, say, for a foot and a half above the level of the ground with netting of a close mesh, or by coating them with some deterrent substance or wash which would prevent the beetles from laying on them. A repellant wash, such as that mentioned in Mr R. N. Chrystal's paper⁽¹⁸⁾ on the "Poplar Borer," *Saperda calcarata* Say, might prove useful. The formula is—

In six gallons of saturated solution of washing-soda dissolve one gallon of soft-soap, add one pint of carbolic acid, mix thoroughly; slack enough lime in four gallons of water, so that when added a thick whitewash will result, then add one half-pound of Paris green; mix thoroughly.

NATURAL ENEMIES.

The larva of *S. carcharias* is parasitised by an Ichneumonid larva. The *Saperda* larva is attacked while boring the horizontal portion of its gallery. One parasitic larva is found on each host larva. The cocoon spun by the former prior to pupation, may be discovered in the portion of the tunnel which the latter had completed before its death.

From the comparatively small number of cocoons found, it did not appear that this Ichneumon was very common in this area. Throughout the investigations no instances of fungus-parasitism were observed either on adults or larvae. In the province of Gerona, Spain⁽¹⁷⁾, however, an Entomophagous fungus has recently been found destroying both adults and larvae of this Longicorn.

In a note on the "Planting of poplars at Kininvie," Banffshire, Scotland, published in the *Transactions of the Royal Scottish Arboricultural Society*, of January, 1919, attention is drawn to the fact, that the cultivation of poplars for economic use has been very much neglected in this country in the past, and that the question of their cultivation is as yet in the experimental stage. It is certain, however, once the possibilities of the various species as economic forest trees have been

definitely proved, that they will be more extensively planted in the future. Of all the more importance, then, both to forester and nurseryman, is the intensive study of this possible deadly enemy.

In conclusion it is with great pleasure that I acknowledge the advice, encouragement and facilities granted me by Dr R. Stewart McDougall in the carrying out of this work.

I am also indebted to Miss Clark, artist, Edinburgh, for the painting of the two coloured figures.

I particularly wish to express my thanks to the Carnegie Trust for the Universities of Scotland, for grant to cover artist's fee and cost of the reproduction of the figures.

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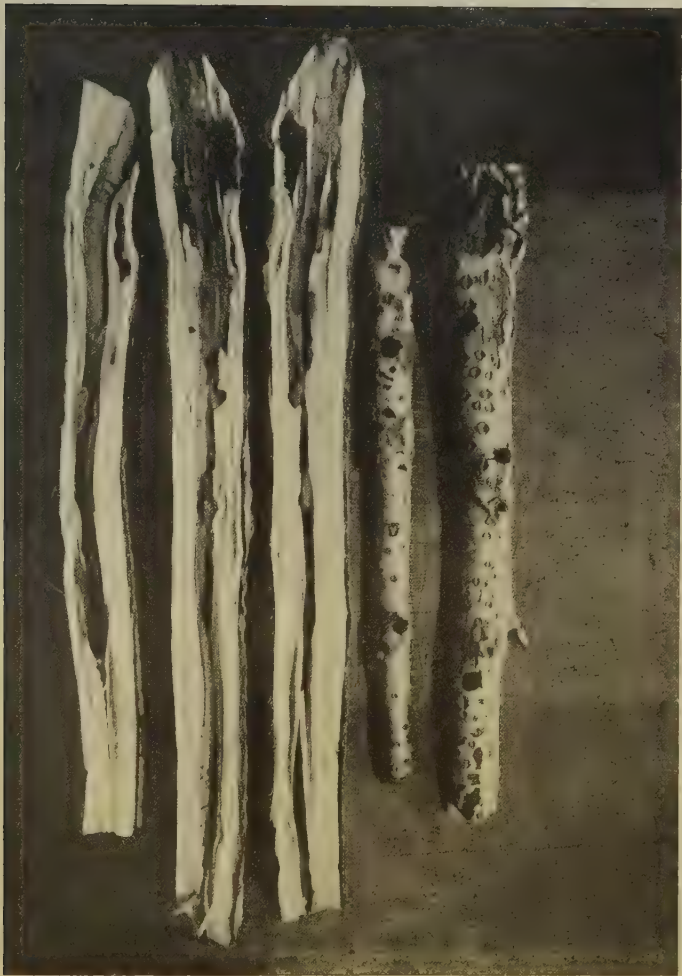
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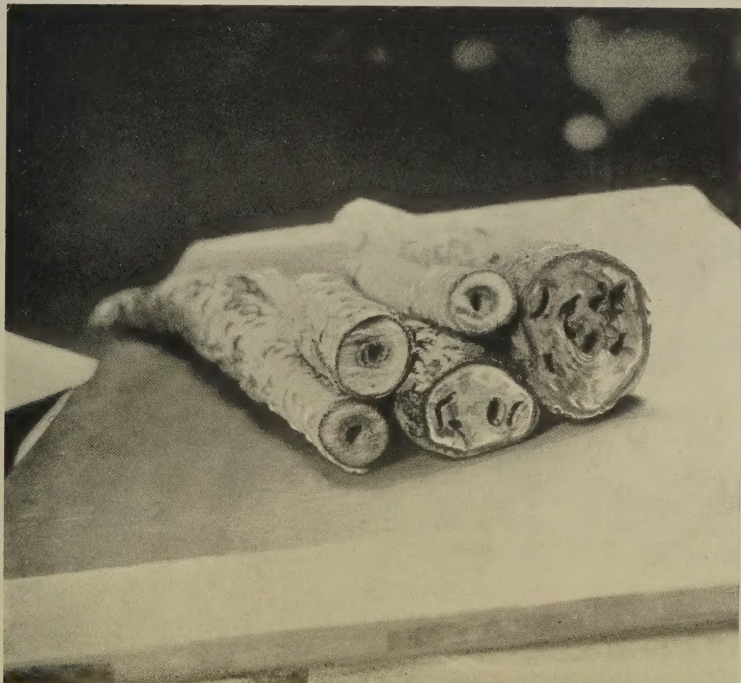


On the left: *Saperda carcharias* Linn., male (ash-grey variety) at rest on a twig of *Populus tremula* Linn.

On the right: *Saperda carcharias* Linn., female at rest on a leaf of *Populus tremula* Linn.

The figures illustrate how the colouration of the beetles is to some extent effective as a means of concealing them.





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DESCRIPTION OF PLATES.

PLATE XX.

On the left: *Saperda carcharias* Linn., male (ash-grey variety) at rest on a twig of *Populus tremula* Linn.

On the right: *Saperda carcharias* Linn., female at rest on a leaf of *Populus tremula* Linn.

The figures illustrate how the colouration of the beetles is to some extent effective as a means of concealing them.

PLATE XXI.

10-12 year old infested stems showing flight holes of adults above, and tunnels of larvae below. The flight holes are round in shape.

PLATE XXII.

Transverse sections of poplar stems badly tunnelled by larvae of *S. carcharias*. The diameters of the sections are as follows: lower row, left to right, 1", 3" average, 4" approx. Upper row, left to right, 1½", and 1½" approx. Tunnels in centre of sections average in diameter ¾".

PLATE XXIII.

Stem of 35 year old poplar, showing fissuring of bark consequent on earlier attack by larvae of *S. carcharias*.

REVIEW.

Insect Pests and Fungus Diseases. By P. J. FRYER. (Cambridge University Press, 1920. 45s. net.)

A book dealing somewhat exhaustively with the pests, zoological and fungoid, of fruit and hops, with the requisite attendant mechanical and chemical appliances and their use in combating them. The whole design of the work is evidence of the author's intent towards its practical use by cultivators, as evidenced by the classification of the material therein contained into headings embracing every detail for rapid reference. It is also happy in not pre-supposing that every grower has found time or inclination for the possession of knowledge on entomology or plant structure.

There are subtleties with regard to insects of economic importance that must be left for elucidation by the entomological expert, and translated by him into broad methods of treatment for the grower, who ever considers control before nomenclature and details; nevertheless accuracy is worth something for its own sake, and the entomologist, as such, will not be disposed to overlook the much useful information for the practical man contained in this book, because of such things as the common wasp being termed *Vespa crabro* and there being some originality in insect classification under the heading of "scientific."

The chemical side, with apparatus, is quite adequately dealt with in a most useful way, and there are calendars and tables, including capacity and quantitative estimation results, that cannot fail to be of value.

The work is full of illustrations, some coloured. A number of those derived from the camera are likely to prove a useful aid to identification of the subjects with which they deal, but the same cannot be said of the reproductions from drawings, which detract from the appearance of the work, which in this respect requires to be again judged by the counter-balance of other matter.

In a second edition the author would find it an advantage to do some re-editing in collaboration with an entomologist.

It should have been noted above that this review has been made solely from the entomological standpoint.

R. S.